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## MEASUREMENT OF ENGELMANN SPRUCE BEETLE POPULATIONS

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The Engelmann spruce beetle, *Dendroctonus engelmanni* Hopk., is a primary enemy of Engelmann spruce, *Picea engelmannii* Parry. Its life history and behavior have been intensively studied. The reasons for the rise and fall of outbreaks, however, are not specifically known. In the study of these fluctuations the measurement of the insect populations in the trees must be accurate and useful. The problem then is one of sampling, and this can be extremely complicated.

The first requirement in sampling the bark beetle population is to obtain a reliable estimate of the number of beetles. Secondly, this must be done with as simple a procedure as can be developed. Since these facts were recognized at the start of the project, the methods developed are accurate and applicable to field use.

At the start, 2 assumptions were made. First, it was believed unnecessary to measure or estimate the beetle population in a tree or area. Instead, the population at one location on a tree was estimated. Second, the fluctuations found at this location were assumed to be similar to the fluctuations elsewhere in the tree.

Certainly there are other systems of sampling applicable to this situation. However, the method developed here is practical and does give the information required on the trends in infestations.

### NUMBER OF BEETLE ATTACKS[2]

Before proceeding with a description of the sampling procedure, we need to know how many beetles attack a tree to determine whether the assumptions expressed are valid. This requires the sampling of attacks (not beetles) over the entire bole of numerous trees. Studies of beetle populations were made on trees in 2 areas in Colorado (Knight 1958, Nagel *et al.* 1957). The data were very much alike. The distribution as expressed by Knight (1958) was used in these current computations. His samples were spaced at 5-foot intervals along the bole. The distribution (Nagel *et al.* 1957) was the same, but data were collected at 8-foot intervals; thus, the 2 sources could not be combined.

An infested[3] tree of 20 inches[4] diameter at breast height is infested to a height of about 35 feet. These figures are based on surveys and on research by entomologists (Knight 1958, Massey *et al.* 1954, Nagel *et al.* 1957). Diameter at 35 feet is about 15 inches. Taper from breast height to 35 feet is uniform. Number of attacks per square foot and per tree are shown in Table I.

TABLE I. Computed numbers of attacks for a spruce tree 20 inches in diameter infested to a height of 35 feet

| Height of 5-ft. bolt from the ground (ft.) | Mean diameter of bolt (inches) | Attacks per sq. ft. | Surface area of bolt (sq. ft.) | Attacks per bolt |
|---|---|---|---|---|
| 0-5 | 22 | 6.6 | 28.8 | 190.1 ±15.8[1] |
| 5-10 | 20 | 5.6 | 26.2 | 146.7 ± 9.4 |
| 10-15 | 19 | 4.7 | 24.8 | 116.6 ± 7.9 |
| 15-20 | 18 | 4.3 | 23.6 | 101.5 ± 8.7 |
| 20-25 | 17 | 3.5 | 22.2 | 77.7 ± 9.5 |
| 25-30 | 16 | 3.1 | 21.0 | 65.1 ±10.1 |
| 30-35 | 15 | 2.7 | 19.6 | 52.9 ± 9.6 |
| Total | | | | 750.6[2] ±68.1 |

[1] Standard error.
[2] Round to 750.

The number of attacks per tree decreases as the diameter and height of infestation decrease. For example, the number of attacks on a 10-inch

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[2] The definition of attack as used here refers to the entrance of an egg gallery or the act of making the entrance.

[3] An infested tree is one that has been attacked by bark beetles and is dying because of the infestation.

[4] Twenty inches was selected for the example because this is close to the average as found in the infestations that have been studied.

tree infested to a height of 25 feet is approximately 250.

The computed number of attacks, bolt and tree, shows variations between trees and between locations within the bole. Entrance holes per tree (750) can be converted to the number of attacking beetles by doubling the number.

## Beetle Numbers in the Basal 5-Foot Bolt

The Engelmann spruce beetle has numerous natural enemies of which the most important may be the woodpecker (Knight 1958). This predator is so effective that insect survival after one year may be negligible above 5 feet from the ground. Below this height the woodpecker work is less, and at the 2-foot level there is seldom any evidence of woodpecker activity. Since survival is greater in the basal 5-foot bolt, this bolt was sampled at the 2-foot level on 100 infested trees (25 from each of 4 locations). Sampling was done when the beetles were in the callow adult stage and shortly before they emerged prior to hibernation. This stage occurs in late August and early September of the year following attack.

Survival averaged 38.9 beetles per square foot at the 2-foot level. Assuming that this rate of survival persists throughout the lowest bolt, 1,120 beetles would emerge from the basal 5 feet of a 20-inch tree. This is more than would actually emerge because beetle survival decreases between 2 feet and 5 feet. It shows that, on the average, insufficient beetles are produced in the lowest 5-foot bolt successfully to attack a tree of the same diameter. An unknown percentage of the beetles die[5] during the following winter while in hibernation and during the spring flight. Studies are in progress on mortality during hibernation. Mortality during spring flight will be much more difficult to evaluate.

## Distribution of Population Samples

Engelmann spruce beetle populations in standing trees have been sampled at various points above the 5-foot level. These samples and observations show that population fluctuations at the 5- to 7-foot level are about the same as those higher on the tree (Table II).

Observations have also been made at other heights. The number of living beetles was always less at the higher sampling points than at 5 to 7 feet. For example, in 12 trees felled and sampled at 5-foot intervals on August 16, 1957, living beetles per square foot on trees attacked in 1956 were as follows:

| *Height of sample* | *Beetles per square foot* |
|---|---|
| 5 | 9.8 |
| 10 | 4.0 |
| 15 | 0.4 |
| 20 | 0.8 |
| 25 | 1.8 |
| 30 | 0.6 |
| 35 | 0.4 |

Table II. Number of living beetles at various heights on 25 infested trees attacked in 1957

| Date sampled | Beetles Per Square Foot | |
|---|---|---|
| | 5-7 feet | 18-20 feet |
| September 1957 | 276.7 | 162.9 |
| June 1958 | 33.3 | 11.0 |
| August 1958 | 14.1 | 5.6 |

Below 5 feet, the number of surviving beetles is greater because of reduced woodpecker predation, protection of the beetles by snow cover, the thicker bark, and possibly other factors. The number of living beetles (Table III) as measured at the 5- to 7-foot level can be used in predicting trends.

Table III. Living beetles per square foot on 3 sampling dates for decreasing, static, and increasing infestations.

| Infestation class | Beetles Per Sq. Ft. | | |
|---|---|---|---|
| | Fall[1] | June[2] | August or September[3] |
| Increasing (3 areas) | 156 | 65 | 40 |
| Static (2 areas) | 260 | 34 | 14 |
| Decreasing (8 areas) | 240 | 9 | 2 |

[1] Sampled soon after trees were attacked.
[2] Sampled as soon as snow was gone.
[3] Sampled before emergence for hibernation.

Beetle populations have been measured in 13 areas of infestation since 1953; eight of these were in decreasing infestations; 5 were in infestations that were static or increasing. The number of bark samples 6 x 6 inches removed at each sampling date was 350 in the decreasing infestations and 222 in the static and increasing ones.[6] The number of samples from all areas were not equal because a number of the trees in some areas were "pitch-outs." Data from such trees were not included so most areas are not represented by the same number of samples in the total. Counts of living beetles were obtained by

[5] Probably at least 50% in stands containing uninfested green trees.

[6] Sampling in any one area and one date consists of removing 2 bark samples from each of 25 trees. Samples are removed between 5 and 7 feet from the ground and all brood under and in the bark is counted.

removing 6 x 6 inch bark samples from the tree boles on each date.

### Frequency Distributions

The frequency distributions of the populations found in these samples are shown in Figures 1, 2, and 3. Figure 1 shows the distributions in the fall when the trees were selected and first sampled. The insects were then in the egg and small larval stages. Figure 2 shows the distributions late the following June when the larvae were large. Figure 3 shows the distributions about 2 months later, just before adults emerged before hibernation.

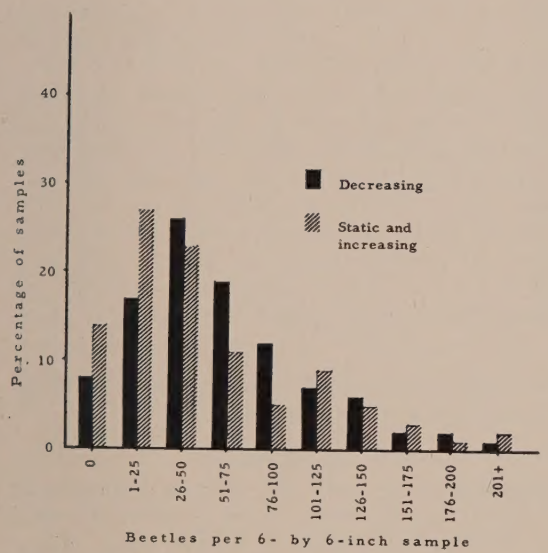


Fig. 1. Distribution of samples. Beetles in egg and small larval stages.

These graphs show that the frequency distributions of the live beetles in the samples change strikingly as the mortality factors reduce the broods. The distributions were similar when sampling was done during the late larval stages and during the adult stage just before hibernation. The same type of distribution is evident for both decreasing and static or increasing infestations.

Waters (1955), Bliss and Fisher (1953), and others show that the negative binomial distribution is applicable to many insect problems of this type. In the negative binomial the variance varies with the mean but disproportionally so. The distribution is a type of "contagious" distribution where the presence of one insect increases the chance of finding others on the same sampling unit. Waters states: "most forest-insect-survey data in the form of counts per sampling unit will

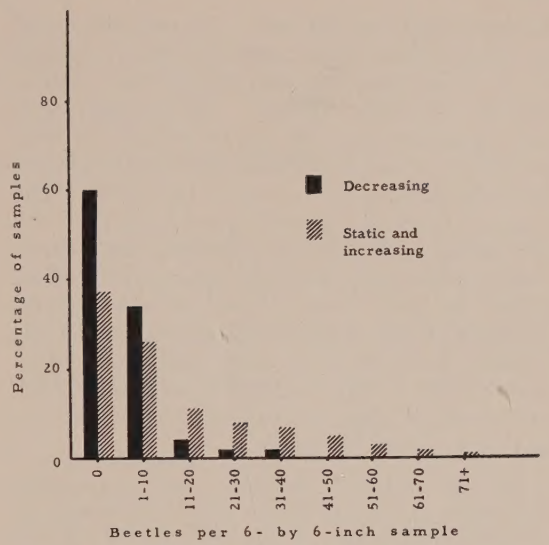


Fig. 2. Distribution of samples. Beetles in large larval stages.

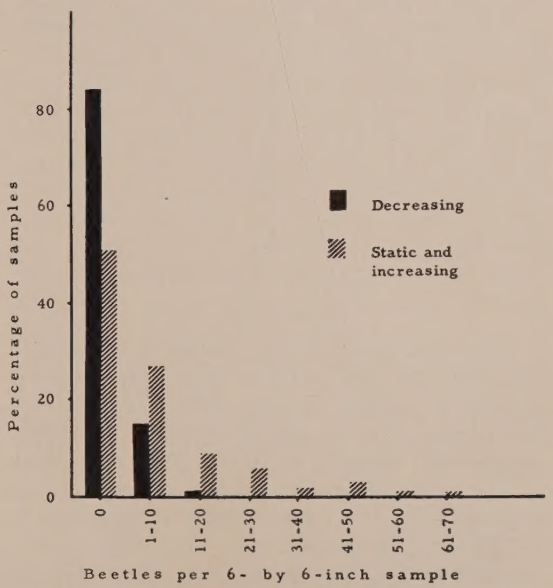


Fig. 3. Distribution of samples. Beetles in adult stage.

follow this distribution." The practical advantage of computing the distribution is for application of a sequential plan for sampling. The sequential plan involves a flexible sample size so that over-sampling or under-sampling can be avoided. A plan that specifies a fixed sample will often result in over-sampling at low and high population levels and under-sampling at intermediate levels.

The negative binomial distribution was fitted to the data from samples collected just before

beetles emerged to hibernate. The procedure used for computing the negative binomial and for testing its fit is described by Bliss and Fisher (1953) and by Anscombe (1949). The estimate of k was computed using the second formula of Bliss and Fisher where k is the constant which balances the formula $k \log (1 + \bar{x}/k) = \log (N/f)$. The negative binomial showed a good fit for both the decreasing and static or increasing infestations. Possibly one of the other contagious distributions might fit even closer. However, the negative binomial is more useful for future application and is easier to handle than other possibilities (Anscombe 1950). The observed data compared with the calculated data for the negative binomial are shown in Tables IV and V.

TABLE IV. Observed distribution and the expected frequencies computed from the negative binominal for decreasing infestations. Mean=0.4257 beetles per 6x6 inch sample.

| Beetles per sample | Observed frequency | Negative binomial calculated frequency |
|---|---|---|
| 0 | 295 | 296.2 |
| 1 | 20 | 25.1 |
| 2 | 18 | 11.1 |
| 3 | 4 | 6.3 |
| 4 | 4 | 3.9 |
| 5 | 4 | 2.6 |
| 6 | 0 | 1.7 |
| 7 | 1 | 1.2 |
| 8 | 1 | 0.9 |
| 9 or more | 3 | 1.0 |

## SUMMARY

Basic information on the number of Engelmann spruce beetles that attack a spruce tree and the number of ensuing progeny in the bole has been developed. The theoretical number of beetles successfully attacking a 20-inch spruce is about 1,500. The number attacking a 10-inch tree is approximately 500. These numbers compared to population data indicate that insufficient beetles are produced in the basal 5 feet of the bole to reinfest a tree of the same diameter. Beetles must be produced and survive in fairly large numbers above the 5-foot level to supply the required number for maintaining an infestation.

Counts of population samples recorded when the beetles are in the adult stage shortly before emergence for hibernation fit the negative binomial distribution. This information should be useful in developing a sequential sampling system for measuring bark beetle populations.

TABLE V. Observed distribution and the expected frequencies computed from the negative binominal for static and increasing Engelmann spruce beetle infestations. Mean=6.7117 beetles per 6x6 inch sample.

| Beetles per sample | Observed frequency | Negative binomial calculated frequency |
|---|---|---|
| 0 | 112 | 112.2 |
| 1 | 17 | 20.8 |
| 2 | 9 | 12.1 |
| 3 | 7 | 8.6 |
| 4 | 4 | 6.6 |
| 5 | 4 | 5.4 |
| 6 | 5 | 4.6 |
| 7 | 4 | 3.9 |
| 8 | 7 | 3.4 |
| 9 | 3 | 3.0 |
| 10 | 2 | 2.7 |
| 11 | 1 | 2.5 |
| 12 | 3 | 2.2 |
| 13 | 2 | 2.0 |
| 14 | 4 | 1.8 |
| 15 | 3 | 1.7 |
| 16 | 3 | 1.6 |
| 17 | 0 | 1.5 |
| 18 | 0 | 1.3 |
| 19 | 1 | 1.3 |
| 20 | 2 | 1.2 |
| 21 | 3 | 1.1 |
| 22 | 1 | 1.0 |
| 23 | 3 | 1.0 |
| 24 | 1 | 0.9 |
| 25 | 1 | 0.9 |
| 26 or more | 20 | 16.7 |

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# THE RELATIONSHIP BETWEEN SEVERAL ENVIRONMENTAL FACTORS AND THE DENSITY OF EUROPEAN CHAFER LARVAE IN PERMANENT PASTURE SOD[1]

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## Introduction

The European chafer, *Amphimallon majalis* (Razoumowsky) (Scarabaeidae) is an introduced pest of turf which has become established in several areas in New York, Connecticut, and West Virginia. The largest of these infested areas include major portions of Wayne, Ontario, and Monroe Counties, New York.

The larvae of the European chafer feed primarily on fibrous root systems and often cause considerable damage to stands of grasses and winter grains. The adults, which are active during June and July, do not feed. They emerge from the soil at sunset, fly to trees, mate, and return to the soil before sunrise. With the exception of these adult nocturnal flights, the entire life cycle is completed in the soil. In New York, one year is normally required for development from egg to adult. There are 3 larval instars, with the 3rd instar larva being the usual overwintering stage.

Burrage and Gyrisco (1954a, 1954b) have demonstrated that the larvae of the European chafer are not distributed at random in permanent pasture sod. The distribution of the larvae more closely approximated a negative binomial than a Poisson series, indicating that there is more clustering of larvae in the soil than would be expected if they were distributed at random. Some of this clustering probably arises because, although deposited singly, the eggs are laid in small groups in the soil.

Clustering also could be attributable to environmental factors which might produce differences in the suitability or accessibility to the European chafer of different areas within a field. Certain of these factors have been investigated by Gyrisco *et al.* (1954), who found that areas in fields kept fallow or covered by tall grass contained fewer larvae than areas having a short grass cover. They noted also that larval infestations were usually light in poorly drained locations.

In the course of sampling studies conducted between 1949 and 1958, several environmental factors have been measured alone or in various combinations. The results of these studies have been analyzed in an attempt to determinate the effect each factor may have in augmenting the non-random distribution of larvae of the European chafer, from one area to another, in fields.

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## Proximity to Trees

Many of the fields used as permanent pastures within the region of European chafer infestation in central New York State are less than 10 acres in area. Some trees are commonly scattered around the periphery of each field, and any location within a field is usually within a few hundred feet of a tree.

Evans (1956) found that adults of the European chafer can fly to trees from distances of over 2000 feet. A far greater proportion of the adults reached the trees from near-by release sites, however, than from sites at greater distances. Further studies have been conducted to determine whether adults, as they left the trees to return to the soil, exhibited a similar phenomenon. If they did, more adults and larger subsequent larval infestations would be expected in areas close to trees than at greater distances.

In each of 4 locations, a sod area adjacent to a single prominent tree line was selected for study; no other trees were within several hundred feet. Three locations, designated by the letters A, B, and C, were situated in Wayne County; location D was in Ontario County.

Locations A and B were at opposite ends of a long permanent pasture which extended along the approximately level top of a drumlin. During May, 1952, at both locations, soil samples were taken from within a rectangular area which extended out toward the center of the field for a distance of 300 feet from the tree line and which was 50 feet in width, along the tree line. The 300-foot distance was divided into twelve 25-foot intervals, and 4 samples, each of which was one square foot in area, were taken at random from within each of the intervals. The soil removed was sorted by hand and examined for the presence of European chafer larvae.

Location C was sampled in a similar manner during October, 1952. The sampling area ex-

tended across a drumlin so that all 25-foot intervals were at the same elevation on the slope. Location D, sampled during May, 1952, was situated in a flat rectangular field. The sampling procedure was modified from that used at Locations A, B, and C; the width of the sampling area, parallel to the tree line, was increased to 200 feet, and 8 one-square-foot units of soil were taken within each 25-foot interval extending into the field from the tree line.

The results obtained are listed in Table I. The larval infestation in each interval of each location has been expressed as a percentage of the total number of individuals found at that location. This procedure places the results obtained at each

TABLE I. The relationship between European chafer larval density and the proximity of the area sampled to trees. Wayne and Ontario Counties, New York. 1952. Correlation coefficient for the regression of average percentage infestation on the distance from trees: 0.6291 (significant at .5 percent)

| No. of feet from tree line | Location A | | B | | C | | D | | Average % |
|---|---|---|---|---|---|---|---|---|---|
| | Larvae[a] per sq. ft. | % of total | Larvae[a] per sq. ft. | % of total | Larvae[a] per sq. ft. | % of total | Larvae[b] per sq. ft. | % of total | |
| 0-25 | 7.25 | 10.70 | 10.75 | 14.33 | 8.25 | 7.64 | 3.13 | 5.83 | 9.63 |
| 25-50 | 7.00 | 10.33 | 15.25 | 20.33 | 8.25 | 7.64 | 2.38 | 4.44 | 10.69 |
| 50-75 | 8.75 | 12.92 | 8.00 | 10.67 | 9.25 | 8.56 | 4.75 | 8.85 | 10.25 |
| 75-100 | 4.25 | 6.27 | 5.00 | 6.67 | 6.25 | 5.79 | 3.75 | 6.99 | 6.43 |
| 100-125 | 5.25 | 7.75 | 13.00 | 17.33 | 12.25 | 11.34 | 1.88 | 3.50 | 9.98 |
| 125-150 | 5.00 | 7.38 | 3.25 | 4.33 | 7.50 | 6.94 | 3.75 | 6.99 | 6.41 |
| 150-175 | 8.00 | 11.81 | 1.50 | 2.00 | 11.25 | 10.42 | 5.50 | 10.25 | 8.62 |
| 175-200 | 6.00 | 8.86 | 4.50 | 6.00 | 9.50 | 8.80 | 5.25 | 9.79 | 8.36 |
| 200-225 | 7.25 | 10.70 | 3.25 | 4.33 | 13.25 | 12.27 | 4.25 | 7.92 | 8.81 |
| 225-250 | 3.75 | 5.54 | 4.00 | 5.33 | 8.75 | 8.10 | 5.88 | 10.96 | 7.48 |
| 250-275 | 2.50 | 3.69 | 4.00 | 5.33 | 7.25 | 6.71 | 6.63 | 12.36 | 7.02 |
| 275-300 | 2.75 | 4.06 | 2.50 | 3.33 | 6.25 | 5.79 | 6.50 | 12.12 | 6.33 |
| Total: | 67.75 | | 75.00 | | 108.00 | | 53.65 | | |

[a] Average of 4 one-square-foot samples.
[b] Average of 8 one-square-foot samples.

of the 4 locations on an equal basis, independent of the differences in average larval densities from one field to another.

## Other Environmental Factors

Among the environmental factors which could affect the distribution of the European chafer in the soil are moisture, soil type and texture, pH, organic matter content, and the slope of the field. The data obtained in the sampling studies presented below, in which one or more of these factors were measured, have been analyzed using multiple regression procedures. Numbers of larvae found in samples have been transformed to logarithms so as to make the data more nearly meet the assumptions required in regression analyses.

In general, the procedure used was as follows: Plots were laid out in permanent pastures and were sampled for an estimate of larval population densities. Soil samples were taken from the same plots and were analyzed for certain physical or chemical properties. The pH was determined with a Model G, line-operated, Beckman pH meter. A modification of the Walkley-Black method, in which the carbon content is determined by the amount of reduction of dichromate obtained, was used for the estimation of percentage organic matter. The moisture equivalent, which is indicative of such soil characteristics as texture, colloidicity, compaction, and organic matter, was measured by the percentage of water which the soil retained when centrifuged at 1000 gravities. Soil moisture content, except where otherwise specified, was measured as a percentage of soil dry weight.

During October, 1952, 4 one-square-foot samples of soil were taken at random from within each of 30 plots located on the eastern slope of a drumlin in Ontario County, New York. The plots, each 25 by 50 feet, were arranged in 4 rows. Two parallel rows of plots extending across the slope were intersected by 2 parallel rows of plots extending down the slope. The data obtained from larval samplings and environmental factor determinations are included in Table II. The relative position of each plot on the slope is indicated by a code number, with number one representing those plots closest to the brow of the hill and number 7 those nearest the base.

During the summer of 1951, 16 plots, each 20 feet square, were laid out in a permanent pasture in Ontario County. Four of the plots were sampled in early August during the time first instar larvae were abundant, 4 were sampled in late August when 2nd instar larvae were present, and 4 each were sampled in November and May during the time 3rd instar larvae were present. One-square-foot soil samples were taken from 4 randomly selected locations in each plot. The sampling data and results of soil moisture and pH determinations are listed in Table III. An average regression of the logarithm of the number of larvae upon soil moisture and pH was obtained by the method of multiple covariance. This procedure placed the results of the 4 sampling dates on an equal infestation basis and permitted the pooled results of the 4 separate regressions to be tested.

If differing soil types or textures are involved, percentage of dry weight may be an inefficient scale on which to express soil moistures when working with biological responses. A clay soil

TABLE II. The relationships between European chafer larval density and soil moisture equivalent, percentage organic matter, pH, and the relative position of each sampling area on the slope of a hill. Ontario County, New York. 1952

| Number of Larvae Per 4 Sq. Ft. | | Soil pH | Percent organic matter | Relative position on slope | Moisture equivalent |
|---|---|---|---|---|---|
| Actual | Log | | | | |
| 20 | 1.30 | 6.10 | 2.7 | 1 | 14.88 |
| 17 | 1.23 | 5.35 | 2.2 | 2 | 13.20 |
| 19 | 1.28 | 5.60 | 1.9 | 3 | 13.46 |
| 26 | 1.42 | 6.00 | 1.9 | 4 | 13.47 |
| 49 | 1.69 | 5.90 | 1.9 | 5 | 13.44 |
| 27 | 1.43 | 5.85 | 2.0 | 6 | 13.48 |
| 38 | 1.58 | 6.10 | 2.1 | 7 | 13.01 |
| 19 | 1.28 | 5.75 | 2.5 | 1 | 14.11 |
| 15 | 1.18 | 6.25 | 1.9 | 2 | 13.98 |
| 36 | 1.56 | 5.55 | 2.2 | 3 | 14.62 |
| 36 | 1.56 | 5.65 | 2.4 | 4 | 14.61 |
| 49 | 1.69 | 5.70 | 3.0 | 5 | 15.92 |
| 35 | 1.54 | 5.85 | 2.4 | 6 | 13.87 |
| 36 | 1.56 | 5.40 | 2.3 | 7 | 13.01 |
| 12 | 1.08 | 6.15 | 2.4 | 2 | 13.30 |
| 47 | 1.67 | 5.30 | 2.7 | 2 | 13.92 |
| 3 | 0.48 | 6.75 | 1.5 | 2 | 12.41 |
| 1 | 0.00 | 6.65 | 2.1 | 2 | 13.49 |
| 9 | 0.95 | 5.80 | 1.7 | 2 | 13.24 |
| 20 | 1.30 | 5.55 | 2.4 | 2 | 14.65 |
| 31 | 1.49 | 5.85 | 2.4 | 2 | 14.64 |
| 22 | 1.34 | 6.15 | 2.4 | 2 | 14.02 |
| 25 | 1.40 | 5.95 | 2.0 | 6 | 13.55 |
| 18 | 1.26 | 5.65 | 2.2 | 6 | 12.62 |
| 38 | 1.58 | 5.90 | 2.0 | 6 | 12.96 |
| 50 | 1.70 | 5.90 | 1.9 | 6 | 13.05 |
| 57 | 1.76 | 6.05 | 2.5 | 6 | 13.82 |
| 34 | 1.53 | 5.80 | 1.7 | 6 | 13.06 |
| 39 | 1.59 | 5.35 | 2.3 | 6 | 13.53 |
| 69 | 1.84 | 5.80 | 1.9 | 6 | 13.70 |

Results of multiple regression analysis of log (no. of larvae) on pH, percentage organic matter, relative position on the slope, and moisture equivalent:

| | pH | Organic matter | Position on slope | Moisture equivalent |
|---|---|---|---|---|
| Partial regression coefficients: | −0.4804 | −0.0416 | 0.1055 | 0.1902 |
| Stand. partial regression coefficients: | −0.4322* | −0.0368 | 0.5669* | 0.3771* |
| Multiple cor. coefficient:.... | | 0.8094* | | |

* Significant at 5 percent.

containing 30% moisture by weight may retain its water with the same tension, and thus have the same physiological moisture, as a sandy soil containing 8% moisture by weight. The electrical resistance method (Bouyoucos 1954) was adopted for use in 1956. It is a method by means of which the soil moisture can be presented on a scale indicative of its availability to organisms, regardless of the type of soil. The advantages of a similar procedure were appreciated by Maezler (1956) in his work with *Aphodius howitti* Hope, a cockchafer inhabiting sandy and loamy soils in South Australia. Maezler expressed soil moistures on the pF scale, which measures the tension by which the water is held by the soil.

In June, 1956, twelve plots, each 10 feet square, were established at scattered locations on the eastern slope of a drumlin in Wayne County. A

TABLE III. The relationships between European chafer larval density and soil moisture and pH. Ontario County, New York. 1951-2

| Stage sampled | Number of Larvae Per 4 Square Feet | | Soil Moisture Percent | Soil pH |
|---|---|---|---|---|
| | Actual | Log | | |
| First instar | 7 | 0.85 | 20.1 | 7.20 |
| | 36 | 1.56 | 13.3 | 7.10 |
| | 70 | 1.85 | 11.8 | 6.00 |
| | 23 | 1.36 | 8.2 | 7.00 |
| Second instar | 30 | 1.48 | 9.0 | 6.00 |
| | 22 | 1.34 | 10.4 | 6.10 |
| | 5 | 0.70 | 24.1 | 7.25 |
| | 10 | 1.00 | 20.8 | 6.90 |
| Third instar (fall) | 96 | 1.98 | 13.5 | 6.10 |
| | 149 | 2.17 | 9.9 | 6.10 |
| | 60 | 1.78 | 11.7 | 6.65 |
| | 23 | 1.36 | 25.6 | 7.05 |
| Third instar (spring) | 48 | 1.68 | 10.1 | 6.40 |
| | 6 | 0.78 | 24.4 | 7.20 |
| | 45 | 1.65 | 15.9 | 6.45 |
| | 33 | 1.52 | 12.4 | 6.65 |

Results of multiple covariance analysis of log (no. of larvae) on soil moisture and pH:

| | Moisture | pH |
|---|---|---|
| Partial regression coefficients:..... | −0.0248 | −0.4327 |
| Standard partial regression coefficients:..... | −0.4159* | −0.5658* |
| Multiple correlation coefficient:..... | 0.9286* | |

* Significant at 5 percent.

plaster of Paris soil moisture block was buried at a depth of 2 inches in the center of each plot. Wire leads, attached to each block, extended above the soil surface. Readings of the resistance in ohms, between the electrodes within each block, were obtained at frequent intervals with a Model C Bouyoucos soil moisture bridge[2]. The readings were corrected for soil temperature by means of a formula provided by Rowland *et al.* (1954). The logarithm of the temperature-corrected resistance in ohms was found to be approximately proportional to percentage available soil moisture, which varies from 100% when the soil is moistened to about field capacity to zero % at a level of moisture slightly below the permanent wilting point for plants. The average of approximately 46 readings of soil moisture, which were made at each plot throughout the year, is presented in Table IV together with the approximate elevation in feet of each plot above the base of the slope. Nine one-square-foot soil samples were taken from randomly selected locations within each plot during the interval from July, 1956 through May, 1957. The total numbers of immature stages (eggs, larvae, and pupae) of the European chafer found in the samples are included also in Table IV.

[2] Industrial Instruments, Inc., Cedar Grove, New Jersey.

TABLE IV. The relationships between European chafer larval density and soil moisture and elevation of the sampling area above the base of the hill. Wayne County, New York. 1956-7.

| Immature Individuals Per 9 Square Feet | | Elevation in feet | Average Soil Moisture | |
|---|---|---|---|---|
| Actual | Log | | In log ohms | As % available soil moisture |
| 2 | 0.30 | 2 | 2.71 | 100 |
| 2 | 0.30 | 3 | 2.90 | 90.5 |
| 29 | 1.46 | 10 | 3.21 | 64.5 |
| 52 | 1.72 | 13 | 3.53 | 45.0 |
| 41 | 1.61 | 19 | 3.37 | 54.0 |
| 70 | 1.85 | 27 | 3.60 | 41.5 |
| 51 | 1.71 | 40 | 3.47 | 48.5 |
| 85 | 1.93 | 48 | 3.36 | 54.5 |
| 46 | 1.66 | 55 | 3.39 | 53.0 |
| 23 | 1.36 | 61 | 3.36 | 54.5 |
| 34 | 1.53 | 67 | 3.47 | 48.5 |
| 53 | 1.72 | 70 | 3.49 | 47.5 |

Results of multiple regression analysis of log (no. of immature individuals) on elevation in feet and moisture in log ohms:

| | Elevation | Moisture |
|---|---|---|
| Partial regression coefficients: | 0.0001 | 1.9319 |
| Standard partial regression coefficients: | 0.0051 | 0.9133* |
| Multiple correlation coefficient: | 0.9308* | |

* Significant at 5 percent.

## Laboratory Studies

The effects of extremes of soil moisture on European chafer adult survival and oviposition, and on the viability of eggs, were examined in the laboratory. Five hundred grams of sifted, oven-dried, loam soil were placed in each of 40 one-quart, screw-capped jars. A predetermined moisture level was established in each jar by the addition of a measured amount of distilled water, followed by gentle shaking. The moistures used were 0, 3, 6, 9, 12, 15, 18, and 21% of soil dry weight. Zero and 3% were below the range of available soil moisture; 21% was at approximately field capacity. One jar of each moisture level was placed in each of 5 constant temperature cabinets, which were maintained at 10, 15, 20, 25, and 30°C. On July 18, 1958, five male and 5 female adults of the European chafer were placed in each jar. At 3-day intervals thereafter, the soil was hand-sorted for eggs and adults. All live adults were replaced in the jars.

The adults died very rapidly in the soil maintained at 0% moisture; longevities at all other moisture levels were considerably higher. Females were found to live significantly longer than males, supporting similar observations by Evans and Gyrisco (1959). The total number of eggs laid by the 5 females in each jar is listed in Table V.

In further studies, 20 eggs were maintained at each of 14 soil moisture levels ranging, in 2% increments, from two to 28% soil moisture by weight. The eggs were incubated at the 5 constant temperatures listed earlier. At 15, 20, 25, and 30°C, at least 50% of the eggs hatched at all moisture levels above 2%. None of the eggs maintained at 10°C had hatched after 82 days. All of the eggs exposed to 2% soil moisture by weight desiccated and failed to hatch.

TABLE V. Number of eggs laid by groups of 5 females of the European chafer confined at constant temperatures and soil moistures.

| % moisture by weight | Temperature in Degrees C | | | | | Total No. of Eggs | |
|---|---|---|---|---|---|---|---|
| | 10 | 15 | 20 | 25 | 30 | Actual | Log |
| 0 | 0 | 0 | 0 | 0 | 7 | 7 | 0.85 |
| 3 | 13 | 2 | 17 | 12 | 7 | 51 | 1.71 |
| 6 | 8 | 34 | 17 | 57 | 33 | 149 | 2.17 |
| 9 | 17 | 24 | 48 | 75 | 60 | 224 | 2.35 |
| 12 | 9 | 24 | 9 | 46 | 17 | 105 | 2.02 |
| 15 | 25 | 28 | 24 | 46 | 39 | 162 | 2.21 |
| 18 | 0 | 38 | 15 | 35 | 31 | 119 | 2.08 |
| 21 | 3 | 12 | 26 | 14 | 17 | 72 | 1.86 |

Regression analysis for log (no. of eggs) on moisture:

| Source of variation | d.f. | M.S. | F |
|---|---|---|---|
| Linear | 1 | 0.4516 | 10.43* |
| Quadratic | 1 | 0.8903 | 20.56* |
| Residual | 5 | 0.0433 | |
| Multiple correlation coefficient: | | 0.9280* | |

* Significant at 5 percent

Twelve eggs were kept covered continuously by distilled water at a temperature of 20°C. All eggs were less than 4 days old when they were submerged. Five of the eggs hatched successfully, with an average incubation period of 30 days. As might be expected, the newly hatched larvae were found dead.

## Discussion

A linear regression analysis of the average percentage of the European chafer larval population found in each of the twelve 25-foot intervals away from tree lines revealed that the larval densities decreased significantly as the distance from trees was increased (Table I). This average trend was sufficiently pronounced to be evident, even though the results at Location D showed an opposite tendency. Some of the large variability found among and within locations may have been due to the action of other, unmeasured environmental factors in the soil. The pooling of the sampling results for 4 locations tends to average out these other factors and to make more evident the influence of the proximity of trees on larval infestation levels.

For the data in Tables II and III, the relationships between the various environmental factors and the logarithms of larval numbers have been presented in the form of standard partial regres-

sion coefficients. Since these coefficients are independent of the original scale of measurement, they may be compared directly to obtain an estimation of which of the environmental factors, if considered independently of the other factors, could give the best prediction of the size of larval populations which might be produced in a given area.

Soil moisture can have a preponderant effect on the densities of European chafer larvae in permanent pasture sod. However, it would appear that perhaps moist soils are not severely limiting to larval populations except in those areas where the soil moisture remains near or above the level of field capacity for long periods. This effect was observed in the two wettest plots shown in Table IV; two eggs were found in each of those plots in August, and no further eggs, larvae, or pupae were found there in the following 8 samples taken during the remainder of the study. A number of similar sampling studies have been conducted which are not described here. Typically, if very damp places were located within the area sampled, fewer larvae were found there; usually if no very damp places were present, no correlation between larval numbers and soil moisture was detected.

Results of the laboratory studies indicate that eggs of the European chafer are relatively resistant to high soil moistures. However, more eggs were laid by adults at the median moisture levels, within the range of available soil moisture, than in very wet or dry soils (Table V). In the field, there are indications also, that as the larvae mature, the proportion of them found in the wettest areas as compared with that in drier areas remains about constant (Table III). Therefore, the low larval infestations found in wet soils may reflect both a low number of eggs laid in such areas and a high mortality of newly hatched larvae.

The permanent pastures in central New York are usually located on land of marginal value and often are inadequately limed and fertilized. Larval densities were found to be correlated with the soil acidity (Tables II and III), with the highest infestations occurring in the more acid soils. Soil moisture also was highly correlated with pH; this might be expected, since the best drained areas would tend to be more highly leached and would therefore be more acid than poorly drained areas. Nevertheless, the significant standard partial regression coefficients for both moisture and pH (Table IV) indicate that each of these factors produced an independent effect on larval densities. The results of these and other studies which have been examined indicate that the degree of acidity may be most important in the wetter soils; in soils which remain generally dry there may be less effect of pH on population densities of European chafer larvae. It is of interest to note that liming, as well as being a worthwhile agronomic practice, might contribute toward reducing the levels of European chafer populations. In addition, the more vigorous grasses which would be produced in adequately limed areas would probably be better adapted to survive larval damage than would less vigorous plants. A similar influence of pH has been described by Hammond (1949), in his work with *Phyllophaga* spp. He found indications that adult oviposition was heavier and larval survival higher in slightly acid soils than in more alkaline soils.

The sampling results presented in Table II indicate that larval densities were correlated with slope, with more larvae being found on the lower than on the upper portions of the slope. This relationship is in doubt, however; in a large number of other sampling studies, no consistent effect of slope, independent of other environmental factors, on European chafer larval densities has been found. The effect noted in Table II might be the result of a joint correlation among larval densities, slope, and some other unmeasured environmental factors such as soil moisture.

Percentage organic matter content of the soil appeared to have no consistent effect on the densities of larval infestations (Table II).

Repeated observations (Gyrisco *et al.* 1954) have revealed that higher European chafer populations might be expected in light, sandy soils than in heavier soils such as clays. The latter, having a finer basic particle size and a far greater colloidicity, would have the higher moisture equivalent. This relationship has not been studied adequately under controlled conditions, as is evidenced by the results in Table II in which the soils with the highest moisture equivalents contained the highest larval populations.

## Summary and Conclusion

The highest populations of larvae of the European chafer in permanent pasture sod usually were found in those areas which were closest to trees and in soils which had the lowest moistures and pH levels. A measurement of these factors might be of value to an investigator planning a sampling study of European chafer larvae in the field or attempting to predict future European chafer population densities. There are indications that the limiting effect of high soil moistures is exerted most strongly upon the ovipositing adults

and the newly hatched first instar larvae. No consistent relationships have been detected between larval densities and the soil organic matter content, the moisture equivalent, or the location of sampling areas on the slopes of hills.

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# SIZE AND DISPERSION OF A LOUISIANA POPULATION OF THE CRICKET FROG, *ACRIS GRYLLUS*[1]

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## Introduction

The determination of numbers and densities of organisms is one of the fundamental endeavors of ecology, whether this be in the applied field of wildlife management, or in evaluating the role of populations in the trophic structure of communities. Aside from the theoretical value of knowledge of the size and composition of anuran populations, it appears likely that such information will be of most significance as it is related to studies of energy transfers at the community level. In certain communities anurans play an important role as primary consumers and, after metamorphosis, as secondary consumers. It is worthwhile, then, to develop effective methods of obtaining estimates of the size of anuran populations with the same indices of reliability which have been obtained in studies of most other vertebrate groups.

Estimates of the size of anuran populations have been almost invariably based on treatment of capture-recapture data by the proportional index method (Jameson 1955, Martof 1956, Pyburn 1958). Pearson (1955) actually enjoyed better success with "adjusted counts" of spadefoot toads but these animals were in enclosures. Martof also obtained estimates of newly transformed *Rana clamitans* by a quadrat technique, but the variances of the estimates were so great that one can hardly accept them with confidence. Still, this work represents the first indication of confidence limits for anuran population estimates.

There is a considerable literature pertaining to capture-recapture analysis and many of the techniques which have been developed may be applied to data from studies of anuran populations. For example, Bailey (1952) has summarized several procedures related to recapture data. Perhaps the most useful, as far as work with amphibians is concerned, is a means of calculating the variance of the population estimate from conventional recapture data. Schumacher and Eschmeyer (1943) proposed a method (henceforth ascribed to Schumacher) of estimating the size of stable fish populations based on a series of censuses weighted according to sample size. This method has been discussed by Hayne (1949) with reference to mammal populations and by DeLury (1958) with added refinements. This technique has been used in estimates of anuran populations by Pearson (1955), Pyburn (1958) and Turner (1959), but in no case did the authors indicate the variances of the estimates. Methods of estimating mortality rate and population size (and the variances of these parameters) are described in a series of important papers from

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the Oxford Bureau of Animal Population (Leslie and Chitty 1951, Leslie 1952, Leslie, Chitty, and Chitty 1953). There is growing concern as to the validity of certain assumptions underlying capture-recapture analyses and a test for dilution of the population under study by immigration (Leslie 1952) has been developed.

At present, the investigator is faced with several possible methods of treating capture-recapture data. Some methods require more time, both in collecting and analyzing the data, than others. One may wonder whether complex procedures actually yield results superior to those obtained by less elaborate methods. For that matter, is capture-recapture analysis the most efficacious approach? Blackith (1958) has suggested that, in randomly dispersed populations, the density (and hence the population size) may be calculated from the mean nearest-neighbor distance using a formula developed by Clark and Evans (1954). Theoretically, Blackith's procedure is only justified when members of the population examined are distributed at random, so any application of this method must be coupled with an analysis of the dispersion of the population.

The purpose of this paper is to compare various estimates, based on the same capture-recapture data, of the size of a small population of *Acris gryllus,* and to investigate the possibility of estimating the size of the population from nearest-neighbor measurements.

## Methods

The study area was the west end of a cleared field in St. Tammany Parish, Louisiana, about 5 miles south of Covington. This field, grown with various closely-cut grasses and rushes, has been cleared from the surrounding loblolly pine woodland (*Pinus taeda*). Among the pines are a few sweet gums (*Liquidambar styraciflua*) and, as a dominant in the understory, bayberry (*Myrica carolinensis*). Along both the north and south edges of the field are roads; at the west end is uncut woodland. The area was divided into 71 quadrats, each of 25 sq m. In late December of 1958 there were about 500 sq m of standing water in this 1775 sq m, as determined by planimeter measurements from a map of the area (Figure 1). In early April of 1959, the extent of the water was about 700 sq m (Figure 2). The water ranged in depth from about 2 cm to 12 cm with most depths from 5 to 10 cm.

Samples of cricket frogs were taken on December 20, December 24, December 28, December 31, 1958, and January 3, 1959 (these dates henceforth referred to as $t_0$, $t_1$, $t_2$, $t_3$ and $t_4$). Animals

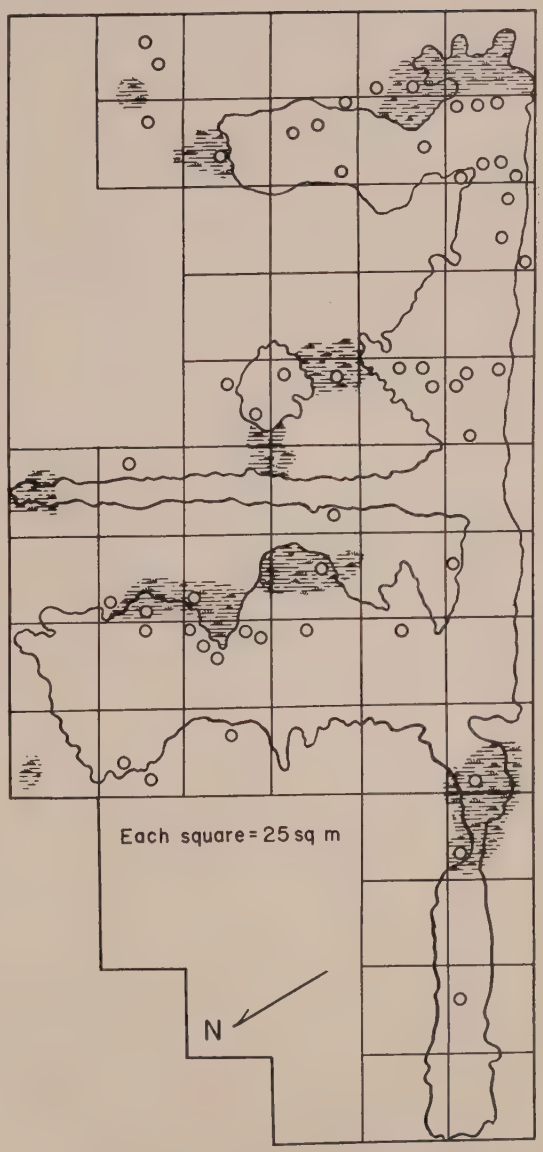


Fig. 1. Dispersion of 54 *Acris gryllus* in a field near Covington, Louisiana, on December 31, 1958. Each circle represents one frog.

captured were marked by excising a toe so as to indicate the time at which they were captured. Thus, at the time of the final sampling, a marked animal could bear a maximum of 4 marks (captured at $t_0$, $t_1$, $t_2$ and $t_3$) or any lesser number of marks, the combination indicating the dates on which the individual was captured. On December 31 the locations of 54 frogs were recorded on a map (Fig. 1) and measurements taken with a cloth tape so that the nearest-neighbor distance for each individual was known. On April 2, 1959, 98 frogs were captured, marked, and re-

FIG. 2. Dispersion of 98 *Acris gryllus* in a field near Covington, Louisiana, on April 2, 1959. Each circle represents one frog.

leased, and their locations recorded (Fig. 2). Measurements were again taken, yielding another series of nearest-neighbor measurements. On April 3, 64 frogs were captured, 49 of which had been marked the previous day.

## CAPTURE-RECAPTURE ANALYSIS

The sampling data collected on each of five days, during the winter, is summarized in Table I. The total sample on a given date is indicated by $R_t$, the number of unmarked animals by $u_t$, and the marked individuals by m. The marked animals are subdivided into groups, with the first of the 2 suffices indicating the last time of capture (Method B of Leslie and Chitty 1951, p. 275), *e.g.* the group $m_{13}$ includes those frogs captured at $t_3$ which were last captured at $t_1$.

TABLE I. Size and composition of 5 samples drawn from a Louisiana population of *Acris gryllus* during December, 1958, and January, 1959. Explanation of symbols in text.

| $t_0$ | $t_1$ | $t_2$ | $t_3$ | $t_4$ |
|---|---|---|---|---|
| | $m_{01}$ 18 | $m_{02}$ 7 | $m_{03}$ 3 | $m_{04}$ 0 |
| | | $m_{12}$ 24 | $m_{13}$ 19 | $m_{14}$ 3 |
| | | | $m_{23}$ 25 | $m_{24}$ 0 |
| | | | | $m_{34}$ 33 |
| | $u_1$ 36 | $u_2$ 6 | $u_3$ 13 | $u_4$ 5 |
| $R_0$ 32 | $R_1$ 54 | $R_2$ 37 | $R_3$ 60 | $R_4$ 41 |

As a preliminary to an analysis of these data one may ask whether, in the course of the study, the population was diluted by immigration. This sort of problem must be faced in almost all analyses of capture-recapture data and, as Leslie (1952) has shown, it is possible to develop a test for dilution from the sort of data set forth in Table I. Unfortunately, it is necessary to group the recaptures in another way (Method C of Leslie and Chitty 1951, p. 276), according to the first time they were captured and marked. If there is no dilution and the death rate is the same for all subgroups of the population, then the expected proportion of individuals originally marked at a particular time should be constant in all subsequent samples. The manner in which a contingency table is drawn up to test whether this is true is explained by Leslie (1952, pp. 385-6). Table II is based on the data in Table I (with the recaptured individuals grouped by Method C). The total $\chi^2$, with 6 degrees of freedom, is 7.30, indicating a probability of about 0.3 that the observed proportions indicate no appreciable dilution.

The application of the proportional index method to the samples drawn at $t_0$ and $t_1$ yield a population estimate of 96 ($32 \times 54/18$). The variance of this estimate may be calculated as described by Bailey (1952): $\mathrm{Var}(N) = 32^2 \times 54 \times 36/18^3 = 341.33$. This yields a standard error ($s_N$) of 18.47. Using a modification of the proportional index suggested by Bailey (to reduce positive bias) the population estimate is 93. The estimated variance is 280.82, and $s_N$ is 16.76 (see Appendix).

TABLE II. Test for dilution of a Louisiana population of *Acris gryllus*. Chi-square for each cell is indicated in parentheses. Total $X^2=7.30$

| | Time Recaptured | | | | |
|---|---|---|---|---|---|
| Time originally captured | $t_1$ | $t_2$ | $t_3$ | $t_4$ | Totals |
| $t_0$ | 18/19.98 (.20) | 18/13.69 (1.36) | 20/22 20 ( 22) | 15/15 17 (.00) | 71 |
| $t_1$ | | 13/13.14 ( 00) | 23/21 30 (.14) | 13/14 56 ( 17) | 49 |
| $t_2$ | | | 4/ 3.0 (.67) | 1/ 2 0 (.50) | 5 |
| $t_3$ | | | | 7/ 7.0 | 7 |
| unmarked | 36/34.02 (.12) | 6/10.17 (1.71) | 13/13.50 (.02) | 5/ 2.27 (2.19) | 60 |
| Totals | 54 | 37 | 60 | 41 | 192 |

TABLE III. Estimation of the size of a Louisiana population of *Acris gryllus* in December, 1958. $X_t$ is the number of marked individuals in the population just before the $t^{th}$ sample is taken, $n_t$ is the number of individuals in the $t^{th}$ sample, and $x_t$ is the number of marked individuals in the $t^{th}$ sample.

| Time | $X_t$ | $n_t$ | $x_t$ | $x_tX_t$ | $n_tX_t^2$ |
|---|---|---|---|---|---|
| $t_1$ | 32 | 54 | 18 | 576 | 55,296 |
| $t_2$ | 68 | 37 | 31 | 2108 | 171,088 |
| $t_3$ | 74 | 60 | 47 | 3478 | 328,560 |
| $t_4$ | 87 | 41 | 36 | 3132 | 310,329 |
| Totals | | | | 9294 | 865,273 |

$N = 865,273/9294 = 93$

The values needed to estimate the population size by the Schumacher method may be extracted from the information in Table I. Table III illustrates the procedure, the estimate being 93. The 95% confidence limits, calculated as described by DeLury (1958), are 82 and 108 (see Appendix).

Several methods of estimating population size from capture-recapture data have been suggested by Leslie (1952). The various methods are based on different theoretical models and it is necessary to select the model to which the population under study most closely conforms. In this case the appropriate model is one in which no assumptions as to the death-rate are necessary but in which it is assumed that no dilution is occurring (see Leslie 1952, pp. 370 *et seq.*). This method will henceforth be referred to as the first Leslie method. The method of calculating the population estimates at each point in the time series $t_0$ to $t_3$ is illustrated on pp. 378-9 (Leslie 1952). The appropriate data pertaining to the present study, drawn from Table I, are shown in the Appendix of this paper. The successive population estimates and their standard errors are (at $t_0$, $t_1$, $t_2$ and $t_3$ respectively: $94.8 \pm 10.7$, $90.8 \pm 8.0$, $94.9 \pm 12.8$, and $74.1 \pm 5.5$.

A more elaborate method described by Leslie, and which is not, strictly speaking, applicable to the data involved in this study, is predicated on the assumption of a constant death-rate and no dilution. This method will be referred to as the second Leslie method. This model would have been appropriate had the samples been separated by equal time intervals, but the data treated here were taken at intervals of 4, 4, 3, and 3 days. Although the sampling was not done in exact accordance with the requirements of this method, the population was estimated in order to see how well the estimate would compare with the others. As a preliminary to estimating the population in this manner, it is necessary to estimate P, the survival-rate (here assumed constant). The estimation of this parameter is described by Leslie and Chitty (1951), and the necessary values may be drawn directly from Table I. The rather lengthly equation, based on a chain of 5 samplings, which is solved by iteration, may be found in Leslie and Chitty (1951, p. 277). The solution of this equation yields an estimate of 0.91 for P. The variance of P was estimated at .000592 so $s_p$ is .024. Then the estimated loss due to mortality and emigration over the time interval $t_0$ to $t_3$ (December 20 to December 31) is 1-P, or $.09 \pm .024$. Having calculated the survival factor, P, and its variance, it is now possible to estimate $N_0$, the size of the population at $t_0$. The form of the equation used is found in Leslie (1952, p. 381) and yields an estimate of 104 for $N_0$. The standard error of $N_0$, $s_N$, was calculated as 4.33.

Applying the proportional index to the data from April 2 and 3 (and using Bailey's correction for bias) yields a population estimate of 127 ($98 \times 65/50$) with a variance of 78.4 and a standard error of 8.9.

## Dispersion of the Population

The dispersion of 54 individuals captured on December 31 is indicated in Fig. 1. When all 71 quadrats (1775 sq m) are considered, the pattern of distribution is not random but clumped. In an effort to eliminate the effect of gross discontinuities in the available habitat, the area considered was reduced to 54 quadrats (1350 sq m) by excluding 17 quadrats of unsuitable habitat

(Fig. 1). The dispersion of 98 individuals captured on April 2 is indicated in Fig. 2. In this case the area was taken as 66 quadrats (1650 sq m) and only 5 quadrats were excluded (Fig. 2). The mean nearest-neighbor distance on December 31 was 1.94 m; on April 2 it was 1.71 m.

The first step in analyzing these data is to determine whether the individuals are randomly distributed. Unfortunately there seems to be no single unequivocal test available. A number of tests are negative—that is, they will establish non-randomness but cannot establish randomness. For example, Clark and Evans (1955) have shown that in a randomly dispersed population the expected proportion of individuals who are each other's nearest neighbor ("reflexive pairs") is .6215. In the December sample, 30 of the 54 individuals (.556) were involved in reflexive pairs; in April, 64 of 98 individuals exhibited this relationship (.653). The mean of these 2 observations (.62) suggests that there is no departure from random expectations with regard to numbers of reflexive pairs.

The number of individuals serving as nearest neighbors to 0, 1, 2, and 3 other individuals has been worked out in a synthetic randomly dispersed population by Clark and Evans (1955), and the proportions of individuals in the *Acris* population playing similar roles may be compared to these values (Table IV). The $\chi^2$ totals, with 3 degrees of freedom in each case, indicate probabilities of better than 0.5 that the observed values agree with those found by Clark and Evans in a synthetic randomly dispersed population. It should be emphasized again that the reflexive relationships and the data set forth in Table IV, although indicating a similarity between the *Acris* population and a randomly dispersed population, are not positive criteria of random distribution. Clark and Evans (1955) have shown that populations of plants known to be contagiously distributed may compare quite closely with random expectations as to numbers of reflexive pairs and numbers of individuals serving as nearest neighbors for varying numbers of other individuals.

One of the attributes of a randomly distributed population is geographical homogeneity (Cottam, Curtis and Hale 1953). This may be tested by subdividing a map of the area studied into equal subsections and comparing the numbers of individuals present in each portion with the expected numbers by means of a Chi-square test. It is assumed that each major subsection will have an equal number of individuals so the expected

TABLE IV. Numbers of frogs serving as nearest neighbors for 0, 1, 2, and 3 other individuals in a Louisiana population of *Acris gryllus*. Data from December 31, 1958, above; from April 2, 1959, below

| | Observed | Expected | $\chi^2$ |
|---|---|---|---|
| 0 | 17 | 16.04 | .057 |
| 1 | 22 | 24.46 | .247 |
| 2 | 14 | 12.15 | .282 |
| 3 | 1 | 1.35 | .091 |
| Totals | 54 | 54.00 | .677 |
| 0 | 29 | 29.11 | .000 |
| 1 | 41 | 44.39 | .259 |
| 2 | 27 | 22.05 | 1.111 |
| 3 | 1 | 2.45 | .858 |
| Totals | 98 | 98.00 | 2.228 |

numbers are the total number of individuals divided by the number of areas into which the map has been divided. Because of the irregular arrangement of the 54 quadrats considered in the December 31 survey it is impossible to subdivide the area into rectangles. However, 3 groups of 18 quadrats were set apart (in two ways) and in neither case did the $\chi^2$ total suggest a lack of geographic homogeneity. When the 54 quadrats were divided into 6 groups of 9 (again in 2 ways) the $\chi^2$ totals indicated probabilities of .13 in one case, and less than .01 in the other, of geographic homogeneity. The 66 quadrats involved in the April survey were subdivided in a number of ways (sometimes unequally, but with the expected numbers in each area prorated appropriately). The Chi-square tests were of two general patterns—those which indicated probabilities of geographic homogeneity on the order of 0.2 to 0.3, and those which indicated very small probabilities ($< .01$) of such homogeneity. The nature of these tests is such that indication of geographic non-homogeneity by any one of a number of tests implies a non-random distribution.

Another test of randomness involves the calculation of a Poisson distribution with a mean equal to the mean density of the individuals in the area studied. A comparison of the distribution of the 54 frogs captured December 31 with a Poisson distribution with a mean of 1.00 is set forth in Table V. The total $\chi^2$ is 7.842 with 2 degrees of freedom, which indicates a probability of very close to 0.02 that the observed dispersion fits the Poisson distribution. A comparison of the distribution of the 98 frogs captured on April 2 with a Poisson distribution with a mean of 2.875 is made in Table VI. In this case, the probability that the observed distribution fits the Poisson is about 0.11. To

TABLE V. Distribution of 54 *Acris gryllus* in 54 quadrats on December 31 compared to a Poisson distribution with a mean of 1.00

| Number of frogs per quadrat | Observed number of quadrats | Expected number of quadrats (Poisson) | $\chi^2$ |
|---|---|---|---|
| 0 | 27 | 19.866 | 2.562 |
| 1 | 15 | 19.866 | 1.192 |
| 2 | 5 | 9.933 | 2.450 |
| 3+ | 7 | 4.335 | 1.638 |
| Totals | 54 | 54.000 | 7.842 |

test the possible influence of quadrat size the quadrats involved in each survey were subdivided into 4 smaller ones. Some of these smaller quadrats could be eliminated as unsuitable habitat. In both cases the new tests had implications comparable to the first ones.

TABLE VI. Distribution of 98 *Acris gryllus* in 66 quadrats on April 2 compared to a Poisson distribution with a mean of 2.875

| Number of frogs per quadrat | Observed number of quadrats | Expected number of quadrats (Poisson) | $\chi^2$ |
|---|---|---|---|
| 0 | 22 | 14.945 | 3.326 |
| 1 | 17 | 22.195 | 1.216 |
| 2 | 13 | 16.476 | 0.733 |
| 3 | 8 | 8.154 | 0.003 |
| 4+ | 6 | 4.226 | 0.745 |
| Totals | 66 | 66.000 | 6.023 |

It is concluded then, that there is lack of geographic homogeneity (and hence lack of randomness) in both the December and April distributions. Furthermore, with $\alpha = 0.05$, the December distribution does not conform to a Poisson distribution while the April distribution does. One need only visualize a Poisson distribution with those quadrats containing larger numbers of individuals concentrated in the same general area to appreciate that this apparent paradox is quite possible (*e.g.* see Fig. 2).

The estimation of population size as a function of mean nearest-neighbor distance is not, in this case, theoretically justified. However, population estimates have been calculated in order to compare them with estimates based on capture-recapture data and thus to determine the influence of non-random distributions on the procedure suggested by Blackith (1958). A transposition of the Clark and Evans (1954) formula ($\bar{r} = \frac{1}{2}\sqrt{\rho}$) is used, where $\bar{r}$ is the mean nearest-neighbor distance and rho is the density of the population. Blackith has pointed out that this equation may be solved for rho: $\rho = \frac{1}{4}\bar{r}^2$ and the density then translated into a population estimate. The December mean nearest-neighbor distance was 1.94 m and the area occupied by the population taken as 1350 sq m. These values give a density of .066 (frogs/sq m) and the total population is then estimated at 90 ($1350 \times .066$). In April the mean nearest-neighbor distance was 1.71 m and the area was taken at 1650 sq m. This gives a density of .085 and a population estimate of 140 ($1650 \times .085$).

## DISCUSSION

The population estimates derived from the winter capture-recapture data do not differ greatly (Table VII). Even the estimate of 104, derived by equations not theoretically applicable to the data, does not differ greatly from the others. It is actually the reliability of the estimates to which attention must be directed. It may be observed that the proportional index (with correction for bias), based on 2 samples, yields an estimate identical to that obtained by the Schumacher method. We know from experience, however, that this result obtains rarely in practice. Indeed, the large variance is indicative of the relative unreliability of the proportional index estimate. In this study, the standard error is on the order of 18%. Pyburn (1958) estimated a Texas population of *Acris crepitans* at about 1173 individuals (1161 with correction for bias). The variance of this estimate is about 13,313 so $s_N$ is on the order of 115.4 (10%). Pyburn also estimated the size of this population by the Schumacher formula at 1053. Jameson (1955) estimated a small colony of *Syrrhophus marnocki* at 42 individuals. The standard error of this estimate is about 5.6 (13%). These findings are reviewed to afford some idea of the reliability of such estimates when actual data are involved. Standard errors of around 10 to 20% indicate fairly well the limitations of the proportional index. The magnitude of the variance estimate, and hence the standard error, is primarily a function of the relative number of marked individuals in the second sample. In April, when 49 of 64 frogs in the second sample were marked, the variance of the population estimate was small enough (78.4) to reduce the standard error to 8.9 or about 7%.

The estimate of $N_0$ (population size on December 20) obtained by the first Leslie method (94.8) has a standard error of 9.5 or about 10%. The other estimate of $N_0$ (104), based

TABLE VII. Size estimates of a Louisiana population of *Acris gryllus* during December, 1958, and April, 1959. Estimates and 95% confidence limits to the nearest integer. Confidence limits have been calculated as $\pm 1.96\ s_N$.

| Date | Proportional index (Lincoln, 1930; Bailey, 1952) | Schumacher estimate (Schumacher and Eschmeyer, 1943; Hayne, 1949; DeLury, 1958) | Leslie estimate I (Leslie, 1952) | Leslie estimate II (Leslie, 1952) | Nearest-neighbor estimate (Clark and Evans, 1954; Hackith, 1958) |
|---|---|---|---|---|---|
| Dec. 20. | 93±33 | 93 (82-108) | 95±21 | 104±8 | 90 |
| Apr. 2. | 127±18 | — | — | — | 140 |

on the second Leslie method, has a standard error of 4.33, or on the order of 4%. The Schumacher method and the first Leslie method give very similar estimates of $N_0$ and seem to be of comparable reliability. The calculation of the Schumacher estimate is somewhat easier, but neither method poses problems. It is unfortunate that the data were not collected so as to permit a true test of the second Leslie method.

At any rate, we may conclude that in estimating anuran numbers the experimental design should include a series of samples. In applying the proportional index to 2 consecutive samples, the standard error of the estimate will be fairly large unless the first sampling is sufficiently intense to insure a large proportion of marked individuals in the second sample. When time is short, 2 intensive samples may be used to obtain a reasonably good estimate, but there can be no check on the validity of the procedure. A series of, say, 5 samples yields a much more flexible array of data—especially if a different mark is used for each census (which is ordinarily no more difficult than repeating the same mark). Furthermore, Leslie (1952) found, by empirical trials, that increasing the number of samples from 3 to 5 reduced the standard error of the population estimate from about 21% to 12% when his maximum-likelihood equations were used.

When possible, it would be desirable to space samples at equal time intervals. When the death-rate may be assumed constant and there is no significant dilution, Leslie's second method may be of value as a means of estimating the death-rate and may also be applied to estimation of numbers.

On the basis of this single trial, it is impossible to claim superiority for either the Schumacher method or the 2 Leslie methods based on maximum-likelihood equations. DeLury (1954, 1958) has expressed misgivings about the maximum-likelihood method, pointing out that the assumptions on which maximum-likelihood equations are based are often not realized. However, in the present study it has been possible to test, at least in part, the fulfillment of the theoretical assumptions involved in the formulation of maximum-likelihood equations. These tests (see Table II) indicate that Leslie's second maximum-likelihood method would have been valid had the samples been drawn at equal time intervals. Insofar as the data involved in the present study are concerned, the somewhat simpler Schumacher method performed as well as the first method proposed by Leslie.

The distributions of the 54 frogs located on December 31 and the 98 located on April 2 were found to be non-random, which is not surprising in view of previous investigations of animal populations. The situation is summarized by Andrewartha and Birch (1954):

> It is generally true, with very few exceptions, that natural populations are distributed nonrandomly and that the departure from randomness is in the direction of excessive patchiness.

In the case of the *Acris* population the departures from random dispersion are by no means extreme—judging by what comparisons may be drawn from studies of the distribution of certain arthropods (Cole 1946, Macfadyen 1952), or of the dispersion of 3 species of plants in a Michigan old-field (Dice 1952, Clark and Evans 1954). Pearson (1955) actually found spadefoot toads (*Scaphiopus holbrooki*) to be randomly distributed in areas of homogeneous habitat in Florida. It appears likely that discontinuities in the habitat are responsible for the non-random distributions observed in the *Acris* population. For example, one may observe the improved fit with a Poisson distribution in April, when there was more standing water in the area. The lack of geographic homogeneity in both dispersions is clearly attributable to the distribution of the most favorable habitat—*i.e.* a long strip of deeper water along the south side of the area. When tests of geographic homogeneity were made, they typically indicated homogeneity when each subsection contained a portion of this strip—they showed non-homogeneity when some of the subsections did not include a portion of the strip. For example, if the 66 quadrats involved in the April survey (refer to Fig. 2) are divided into 6 subsections of 11 quadrats with the long axes of the subsections northeast-southwest, the $\chi^2$ total, with 5 degrees of freedom, is 6.45—a per-

fectly reasonable value. However, if the 6 subsections are arranged with their long axes northwest-southeast the $\chi^2$ total is 17.96. Other tests involving both dispersions gave similar results.

A section of 18 quadrats (a group 6 by 3 in the southeast corner of the area) involved in the April 2 survey has been analyzed in an effort to see whether, in an area of apparently uniform habitat, the dispersion of frogs is random. All tests indicated geographic homogeneity and a Poisson test gave a $\chi^2$ total of 5.17 with 3 degrees of freedom, which indicates a probability of about .16 that the observed distribution actually fits the Poisson. Thus, there are indications that in homogeneous habitats, as in *Scaphiopus,* nonbreeding dispersions of *Acris* are random.

It may also be pointed out that tests of randomness in spatial distributions of animals require more than the application of a Poisson test. Animals may be distributed in groups which conform to a Poisson distribution, and yet the total distribution may not exhibit geographic homogeneity. Similarly, a single test of geographic homogeneity may be inconclusive for reasons outlined above.

The question now arises as to why, if the observed *Acris* dispersions are indeed non-random, the population estimates derived from nearest-neighbor measurements agree so closely with estimates obtained from capture-recapture data (see Table VII). It has been clearly established that non-random distributions may lead to grossly inaccurate population estimates if nearest-neighbor measurements are used. For example, Clark and Evans (1954) present data pertaining to non-random distributions of *Lespedeza capitata, Liatris aspera,* and *Solidago rigida* growing in a Michigan old-field, which, if used to estimate population size on the basis of nearest-neighbor distances, would lead to estimates ranging from about 2 to 4 times the true values. Clark and Evans also discuss the distribution of trees in a small woodlot, and in this case the dispersion is such that the population would be underestimated by about 23% on the basis of nearest-neighbor measurements. Clearly, the degree of non-randomness in the *Acris* distributions is not so extreme. It is possible that some animal populations, though not distributed in a random manner, may still be estimated successfully from nearest-neighbor measurements.

The findings of Blackith (1958) are quite pertinent to this general problem. He found that grasshopper population estimates based on nearest-neighbor distances were only about ¼ to ½ the size of estimates based on capture-recapture data. One would immediately suspect that the grasshoppers were non-randomly distributed. However, Blackith's conclusion that contagious dispersions were not responsible for the failure of the nearest-neighbor method seems quite legitimate since the estimates were much too low. Blackith also concluded, on the basis of experiments with synthetic populations, that "under-dispersion" (too regular distribution) was not likely to have influenced the estimates. This, of course, is a question of degree, as has already been illustrated by the reference to the distribution of woodlot trees.

Even assuming that Blackith's nearest-neighbor estimates were influenced by under-dispersion, the fact remains that the estimates are much less accurate than would be expected (assuming that the capture-recapture estimates are reliable). A brief review of Blackith's findings will illustrate this point. The sizes of 2 mixed populations of grasshoppers were estimated by the proportional index. In the first experiment, Blackith estimated that there were $2009 \pm 586$ grasshoppers in a field of 6400 sq ft. The mean of 50 nearest-neighbor measurements was 1.75 ft, which, when applied to the Clark and Evans formula, yields a population estimate of 523. If there were actually 2009 grasshoppers in the field, distributed randomly, the mean nearest-neighbor distance would be .89 ft. ($\frac{1}{2}\sqrt{\rho}$; Clark and Evans 1954). The *maximum* possible nearest-neighbor distance in such a population would be 1.92 ft ($= 1.0746/\sqrt{2009/6400}$) and this would obtain only if all individuals were spaced so that every grasshopper had 6 equidistant neighbors, 60° apart. Even if one adopts the minimal estimate of the population (1423), the expected mean nearest-neighbor distance would be 1.04 ft and the maximal possible 2.33 ft. Thus, the observed value, 1.75 ft, aside from indicating a possibility of non-randomness due to regularity of spacing, is more indicative of an inability actually to find the nearest-neighbor of some of the grasshoppers selected. A similar situation arose when this sort of experiment was repeated in another locale. Here the population was estimated at $562 \pm 180$ individuals in an area of 322 sq m. The measured mean nearest-neighbor distance, based on 50 measurements, was 57.1 cm. If 562/322 is the actual density and the population is randomly distributed, the mean nearest-neighbor distance should be on the order of 37.8 cm. The maximal possible value, obtained as above, would be 81.3 cm. Adopting the minimal population estimate (382)

gives an expected mean nearest-neighbor distance of 45.9 cm, and a maximum possible distance of 98.7 cm. So in both of Blackith's experiments there is an indication of non-randomness, due to more regular dispersion than random, against which must be weighed the likelihood that true nearest-neighbor distances were not actually obtained because of an inability to find the nearest neighbor in all cases.

Experience suggests that this last is likely to be a problem in almost all experiments with natural populations of mobile animals. Aside from the fact that one cannot find all the members of the population at one time, one cannot even be assured, in most cases, of finding the true nearest-neighbor of any one of a group of selected individuals. Such must have been the case, to some degree, in the *Acris* population. Although, on both December 31 and April 2, respectable proportions of the entire population were taken, the question arises as to what the mean nearest-neighbor distances would have been had it been possible to locate every individual on both occasions. It may be assumed that the mean nearest-neighbor distances would have been reduced. A rather cursory test of the effect of additional individuals on the mean nearest-neighbor distance of December 31 was made by adding 39 imaginary individuals to the population map in a random manner so that 93 frogs were distributed over an area of 1350 sq m. New nearest-neighbor distances were recorded (estimated when necessary) and the new mean distance was on the order of 1.75-1.80 m. If the population size on December 31 is taken at 93 randomly distributed individuals, the theoretically expected mean nearest-neighbor distance may be calculated as 1.90 m. The significance, if any, of departures from this value may be tested by the following formula: $c = \frac{\bar{r}_A - \bar{r}_E}{\sigma \bar{r}_E}$ where $\bar{r}_A$ is the observed mean nearest-neighbor distance, $\bar{r}_E$ is the theoretical value and $\sigma \bar{r}_E$ is the standard error of the theoretical mean nearest-neighbor distance ($= .26136/\sqrt{N\rho}$, with N the number of nearest-neighbor measurements; Clark and Evans 1954). The value c is considered to be distributed normally about a mean of zero with unit variance. Using the data from the December 31 survey $\sigma \bar{r}_E$ is .135. We may readily calculate, then, that, in order to differ significantly from 1.90 m ($\alpha = .05$), the observed mean nearest-neighbor distance, $\bar{r}_A$, would have to be less than 1.64 m ($1.96 = \frac{\bar{r}_A - 1.90}{.135}$). Hence, an observed mean nearest-neighbor distance of about 1.75 to 1.80 m would not differ significantly from the theoretical value of 1.90 m.

On April 2, when about ¾ of the population was captured, the observed mean nearest-neighbor distance (1.71 m) was less than that expected assuming a randomly distributed population of 127 (1.80 m). Had the other individuals been located, the mean nearest-neighbor distance would have been somewhat depressed—but probably not below 1.61 m, the lower limit of the 95% confidence range for the expected value. Although much of this discussion is speculative, and assumes the capture-recapture estimates to be reliable, there is a suggestion that mildly non-random distributions (as evidenced by Poisson tests and tests of geographic homogeneity) might not be exposed as such by the c test of Clark and Evans (1954).

There are 2 possible sources of error (aside from sampling errors) in the use of the nearest-neighbor measurements to estimate the size of the *Acris* population. First, there is a tendency for clumping of individuals due to discontinuities of habitat. This is not extreme in either case and probably was negligible on April 2. This tendency would reduce the observed mean nearest-neighbor distances and increase population estimates. Second, the failure to find every individual has converse effects. The close accord of the estimates of the December population is probably somewhat fortuitous. Here there were definitely 2 sources of errors, apart from the vagaries of sampling—errors which might have been in part compensatory. On the other hand, I would consider these 2 types of error to be rather small as far as the data of April 2 are concerned. On this date a large proportion of the population was located and, except for relatively minor geographic non-homogeneity, the population was randomly dispersed. Under such conditions a series of nearest-neighbor distances may provide a reliable population estimate.

Estimating populations from nearest-neighbor distances is advantageous in that sufficient data may be collected in 2 or 3 days in the field. However, the analysis of the data is laborious and there is always a strong chance that the necessary theoretical assumptions will not be realized. Capture-recapture data require more time to collect but are usually easily processed (*e.g.* by the Schumacher method). It would seem that the most efficient and reliable estimations of mobile populations will usually follow from an analysis of capture-recapture data based on a chain of at least 5 samplings.

## Conclusions

1. Though it may be possible, by means of two intensive samplings, to obtain an estimate of a small anuran population with a standard error of less than 10%, the same effort distributed over, say, 5 different days will give a more flexible array of data. From these data, assuming an appropriate marking procedure, tests of dilution may be made as well as population estimates.

2. When a series of samples are taken, animals should be marked either individually or, more simply, with a different mark for each census.

3. Samples should be drawn at equal time intervals when possible.

4. With the data involved in this study, the Schumacher method performed as well as the somewhat more complex maximum-likelihood methods.

5. The *Acris* colony investigated was not randomly distributed—probably because of discontinuities in available habitat. The departures from randomness were not extreme on either December 31 or April 2 and were probably negligible on the latter date as far as an estimation of numbers from nearest-neighbor distances is concerned.

6. It is concluded that the most effective test of randomness of dispersion is a Poisson test coupled with a number of tests of geographic homogeneity. Neither type of test is conclusive alone.

7. The close accord of capture-recapture population estimates and estimates based on nearest-neighbor distances is due to relatively slight departures from randonmness in the observed distributions of the colony, possibly coupled with two compensatory kinds of errors in the determination of mean nearest-neighbor distances.

8. Although the nearest-neighbor method performed well under the conditions of this experiment, it is concluded that the most efficient method of estimating anuran populations will follow from an analysis of capture-recapture data based on a chain of at least 5 samplings.

## Summary

The efficiency and reliability of several methods of estimating population size from capture-recapture data and from nearest-neighbor distances were tested on a small Louisiana population of *Acris gryllus* during late December of 1958 and early April of 1959.

A chain of at least 5 samples seems to be the best approach to an estimate based on capture-recapture data. The data then permit tests of the fulfillment of some of the assumptions underlying capture-recapture analyses. Such data may be analyzed by the Schumacher method or by whichever of several maximum-likelihood equations seems appropriate. With the data of this study the Schumacher formula performed as well as the more complex maximum-likelihood equations.

An analysis of the dispersions of the colony on December 31 and April 2 revealed them to be non-random. The degree of non-randomness was slight and the estimates of population size based on nearest-neighbor distances agreed closely with capture-recapture estimates. It is concluded, however, that a well-planned capture-recapture program is more efficient, and apt to be more reliable, than an attempt to determine anuran numbers from nearest-neighbor distances.

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## Appendix

1. Bailey's (1952) modification of the proportional index to reduce positive bias:

$$N = a(n+1)/(r+1)$$

a = marked individuals at risk
n = size of second sample
r = marked individuals in second sample

2. For estimating the variance of N (with correction for bias):

$$\mathrm{Var}(\hat{N}) = a^2(n+1)(n-r)/(r+1)^2(r+2)$$

3. For estimating variance ($s^2$) of Schumacher estimate (refer to Table III):

$$(m-1)s^2 = \Sigma x_t/n_t^2 - [\Sigma x_t X_t]^2/\Sigma n_t X_t^2 \qquad (m=4)$$

4. For estimating end-points of confidence range for Schumacher estimate:

$$\Sigma n_t X_t^2/\Sigma x_t X_t \pm t\alpha s\sqrt{\Sigma n_t X_t^2}$$

where $t\alpha$, with 3 d.f. (for 95% confidence limits) = 3.1825

5. For estimating successive $N_t$ from data in Table I. Recaptures grouped according to Method B. (Refer to p. 379; Leslie 1952).

| time orginally captured | Time Recaptured 0 | 1 | 2 | 3 | 4 | $k'_{xt}$ | $N_t$ |
|---|---|---|---|---|---|---|---|
| 0 | | 18 | 7 | 3 | 0 | 64.18 | $\frac{32(192+1)}{64.18+1} = 94.8$ |
| 1 | | | 24 | 19 | 3 | 81.65 | $\frac{54(138+1)}{81.65+1} = 90.8$ |
| 2 | | | | 25 | 0 | 38.75 | $\frac{37(101+1)}{38.75+1} = 94.9$ |
| 3 | | | | | 33 | 33.00 | $\frac{60(41+1)}{33+1} = 74.1$ |
| $R_t$ | 32 | 54 | 37 | 60 | 41 | | |
| $z_t$ | | 2.51 | 2.05 | 1.55 | 1.00 | | |

6. For estimating standard errors of successive estimates of $N_t$ obtained by first Leslie method. (Refer to p. 372; Leslie 1952).

| t | (1) $R_t$ | (2) $\sum_{x+1}^{T} R_t$ | (3) $\sum_{t=x+1}^{T} k'_{xt}$ | (4) $\sum_{t=x+1}^{T} u_{xt}$ | (5) $(\Sigma R_t+1)(\Sigma k'_{xt}+2)$ | (4) ÷ (5) | $N_t\sqrt{(4)\div(5)}$ |
|---|---|---|---|---|---|---|---|
| 0 | 32 | 192 | 64.18 | 164 | 12,772.24 | .0128 | 10.7 |
| 1 | 54 | 138 | 81.65 | 92 | 11,627.35 | .00791 | 8.0 |
| 2 | 37 | 101 | 38.75 | 76 | 4,156.50 | .0183 | 12.8 |
| 3 | 60 | 41 | 33.00 | 8 | 1,470.00 | .0054 | 5.5 |
| 4 | 41 | — | — | — | — | — | — |

# SMALL-MAMMAL POPULATIONS OF A MARYLAND WOODLOT, 1949-1954

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A program to study the effects of soil conservation practices on wildlife was begun at the Patuxent Research Center in 1946. As a major part of this program, an experimental farm was planned with the help of the Soil Conservation Service. A farm woodlot of 4.4 acres was included in these plans, and was delimited when adjacent areas were cleared. An ecological study of small-mammal populations of this woodlot began in August of 1949. The principal objectives were to follow the seasonal and long-term fluctuations of the populations, to determine the habitat preferences of the species, and to find the length of time individuals remained in the area. Live trapping continued at intervals of approximately 2 months until May of 1954, a period of nearly 5 years.

Warbach conducted the study throughout this 5-year period and reviewed the manuscript. L. Stickel analyzed the data, prepared the manuscript, and mapped the vegetation of the woodlot. We are grateful to many individuals for assistance with various phases of the work. Durward L. Allen, Arnold L. Nelson, and Fred H. Dale sponsored the project and made possible the preparation of this report. William H. Stickel helped with interpretation of the ecological history of the woodlot, identified plant species, and made many helpful suggestions concerning the manuscript. Frederick C. Schmid obtained records and photographs of the woodlot and farm and measured the slope of the woodlot hillside. Aelred Geis suggested a statistical method for ad-

FIG. 1. Aerial photograph of woodlot and surroundings, June 1953. The north corner of the woodlot is at the lower left. The north-south line runs diagonally across the woodlot.

justing survival figures. Brooke Meanley permitted the use of some of his unpublished data. John T. Linehan did part of the trapping in February and April of 1953. R. H. Fenton, U. S. Forest Service, Beltsville, Maryland made increment borings to determine ages of trees in the woodlot and also provided data concerning pine seed yield during the years of our study.

## Study Area

The farm woodlot is in the eastern part of the Center, about 1.9 miles north of Bowie, Maryland and 0.3 mile south of the Patuxent River. The woodlot hillside has a slope of 3.7%, and an elevation of about 120 feet. The soil is Tuxedo gravelly sandy loam. Trees of the woodlot began to grow in abandoned fields 25-35 years before the trapping of 1949. Cultivation ridges across the hillside still are perceptible in 1959. The Soil Conservation Service estimated that about 75% of the topsoil was lost by erosion. The woodlot is shown in Figures 1 and 2.

The woodlot is surrounded by cultivated fields, which were in various stages of a wheat-hay-corn rotation. Fields 49 and 44b were in hay throughout the trapping. *Lespedeza bicolor* was planted along the northeast margin in 1948, was well-established and dominant by 1951, and fruited in 1952. *L. cuneata* (sericea) was planted along the southeast side and *L. japonica intermedia* along the southwest side, but both did poorly and were re-planted in 1950 and 1952. They produced a few seeds in 1952. Along the northwest border, woods abutted directly on the field without a transitional shrubby margin.

Pine trees 60-75 feet high in 1959 are dominant over most of the woodlot. Virginia pines (*Pinus*

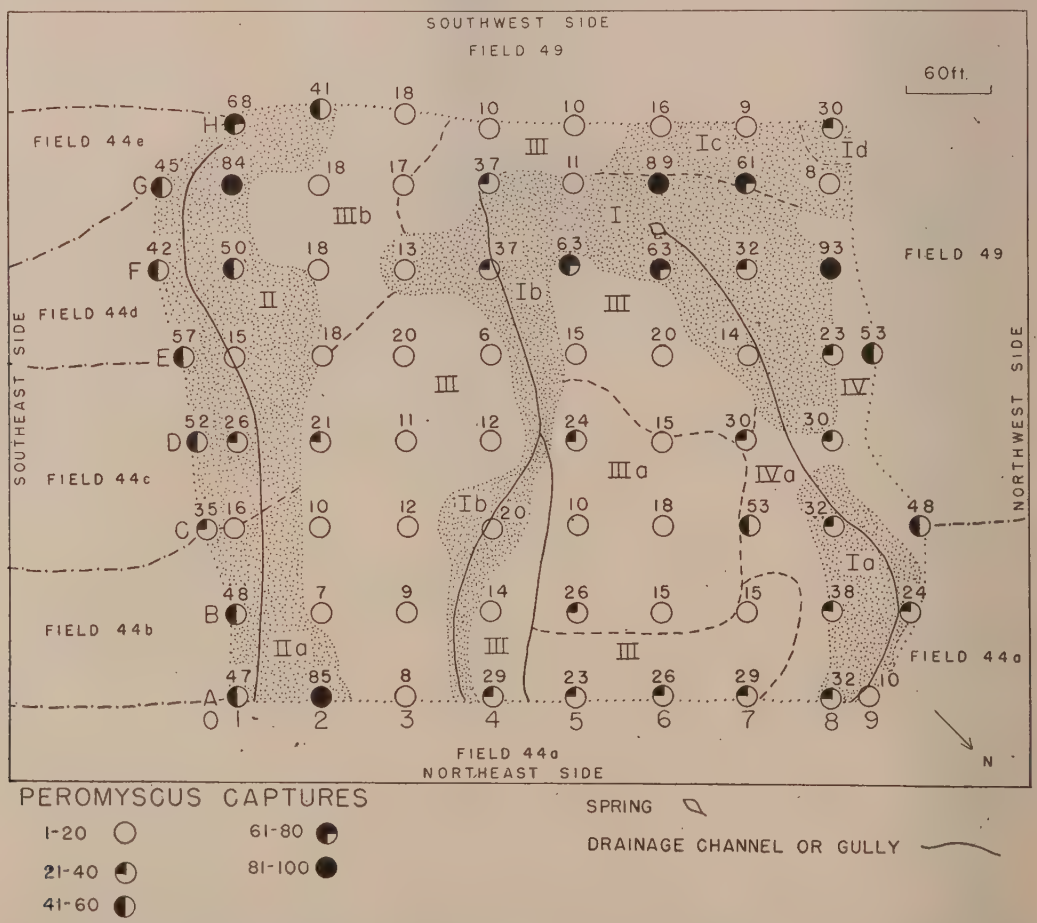


Fig. 2. Map showing vegetation of woodlot, positions of surrounding fields, and distribution of Peromyscus. Deciduous trees were dominant in the areas shown by shading, pine trees in the remainder. Areas marked off by broken lines and labeled with Roman numerals are explained in the text, either in the description of vegetation or in discussions of mouse distribution. Numerals and circles at the trap sites show total numbers of Peromyscus captures, 1949-54.

*virginiana*) are most numerous; pitch pines (*P. rigida*) are occasional. The pine areas shown in Figure 2 differ from each other in age and growth form of trees and in density of the undergrowth as follows: (1) In area III, the larger pines of both species are about 15-20 inches d.b.h.

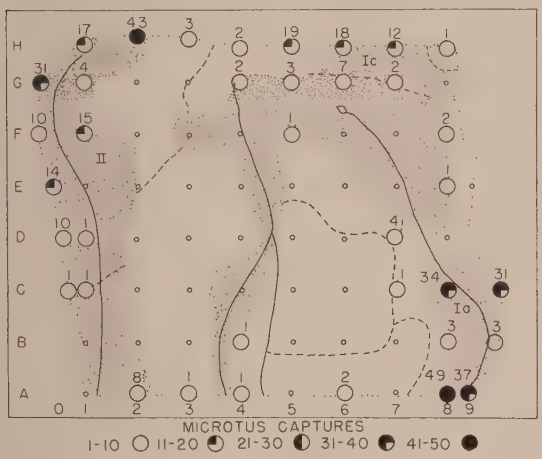


FIG. 3. Map showing distribution of Microtus in the woodlot. Numerals and large circles at the trap sites show the total numbers of captures, 1949-54. Other symbols as in Figure 2.

They are large spreading trees that appear to have grown in the open. Increment borings showed that they were about 25 years old in 1949. Sweetgums of about the same age are scattered among the pines. Younger sweetgums, red maples, and pines are numerous; very young pines are dominant in patches. Undergrowth is sparse; it consists primarily of young trees; highbush blueberry is common locally. (2) In area IIIa, Virginia pines form a nearly pure stand of tall straight trees that apparently grew close together. They are a little smaller in diameter than the larger pines in other parts of the woodlot, but about 10 years younger. Still younger pines are mixed with them. Needles cover the ground completely, and there are many logs from fallen trees. (3) Pines are rather widely spaced in area IIIb. A dense mat of honeysuckle covers the ground. (4) In pine areas IV and IVa, the deciduous undergrowth is moderately dense to very dense. The same undergrowth species are present as in the adjoining deciduous areas.

Deciduous trees are dominant in the moister parts of the woodlot. A variety of species form the undergrowth, which is dense or moderately dense nearly everywhere. There are many dense viny tangles. (1) The greatest variety of trees is in area I, surrounding the spring. Many of the same species grow along the run that flows from the spring to the north corner, Ia. Undergrowth is dense, tangly, and varied. (2) A dense growth of young sweetgum and maple follows from the spring area along a central seepage zone and shallow rain-runoff channel, Ib. There is herbaceous ground cover but no other undergrowth. An erosion ditch branches off from this second seepage area and runs a separate course through the pines to the edge of the woodlot. (3) Very young grassy and herbaceous growth dominated area Ic at the time of trapping. A small clump of young trees and bushes stood at the west corner, Id. (4) Another deciduous zone borders the southeast side of the woodlot; II, IIa. Trees grow on both sides and within an old, deep erosion gulley. A row of older trees, principally pin oaks and sweetgums, follows a former fence line at the edge of the woodlot. Honeysuckle is the dominant ground cover in II and IIa. In area II, it forms a matted layer a foot or more deep and climbs several feet up the bases of most of the trees and climbs over and submerges the young trees, shrubs, and broken stubs.

The principal deciduous trees (names after Fernald 1950) are: sweetgum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), pin oak (*Quercus palustris*), tulip poplar (*Liriodendron tulipifera*), blackgum (*Nyssa sylvatica*), willow oak (*Quercus phellos*), and large-toothed aspen (*Populus grandidentata*). Less common species are: persimmon (*Diospyros virginiana*), black cherry (*Prunus serotina*), flowering dogwood (*Cornus florida*), white sassafras (*Sassafras albidum*), black locust (*Robinia pseudo-acacia*), river birch (*Betula nigra*), sweet bay (*Magnolia virginiana*), holly (*Ilex opaca*), beech (*Fagus grandifolia*) (seedling and shrub height only), and Spanish oak (*Quercus falcata*) (seedling and shrub height only).

Young trees and a few kinds of shrubs form the undergrowth. Japanese honeysuckle (*Lonicera japonica*), and smilax (*Smilax glauca*) are most common; highbush blueberry (*Vaccinium corymbosum*), lowbush blueberry (*Vaccinium vacillans*), and sumac (*Rhus copallina*) are dominant locally, particularly towards the woods edge. Maleberry (*Lyonia ligustrina*), arrow-wood (*Viburnum dentatum*), and other shrubs are more scattered.

## METHODS

The woodlot was trapped during 29 periods of 7 days each. The first period began on August 23, 1949, and the last one ended on May 20, 1954.

TABLE I. History of Peromyscus in the woodlot.

| Period of First Capture | Number of New Mice | Captures in Later Periods[1] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1949 | | | | | | | | | | |
| Aug. 23-29 | 9(8)+2 | 3(2)+2 | 2+1(0) | 2+0 | 0+0 | | | | | |
| Oct. 19-25 | 5+7(6) | 3(2)+4(3) | 1+3 | 0+0 | | | | | | |
| Dec. 13-19 | 5+2 | 4+2 | 0+0 | | | | | | | |
| 1950 | | | | | | | | | | |
| Feb. 8-14 | 0+1 | 0+0 | | | | | | | | |
| Apr. 4-10 | 0+0 | | | | | | | | | |
| June 6-12 | 3+4 | 3(2)+3(2) | 1+2 | 1+2 | 1+2 | 1+2 | 0+0 | | | |
| Aug. 1-8 | 3(2)+1(0) | 2+0 | 2+0 | 1+0 | 1+0 | 0+0 | | | | |
| Sept. 21-27 | 2+1 | 1+0 | 1+0 | 1+0 | 0+0 | | | | | |
| Dec. 15-21 | 12(11)+12 | 7+6 | 5+5 | 1+1 | 1+1 | 1+1 | 1+1 | 1+1[2] | 1+1 | 1[3]+0 |
| 1951 | | | | | | | | | | |
| Feb. 13-19 | 2+2 | 0+1 | 0+0 | | | | | | | |
| Apr. 5-11 | 0+0 | | | | | | | | | |
| June 1-7 | 11+10 | 7+4 | 1+2 | 1+0 | 1+0 | 1+0 | 1+0 | 1+0 | 1+0 | 1+0 |
| Aug. 1-7 | 7+3(2) | 4+2 | 3+1 | 0+1 | 0+1 | 0+0 | | | | |
| Sept. 26-Oct. 2 | 2+1 | 0+1 | 0+1 | 0+0 | | | | | | |
| Nov. 27-Dec. 3 | 11(10)+11(10) | 5+0 | 3+0 | 1+0 | 1+0 | 0+0 | | | | |
| 1952 | | | | | | | | | | |
| Jan. 31-Feb. 6 | 1+3 | 0+1 | 0+0 | | | | | | | |
| Mar. 21-27 | 2+0 | 1+0 | 1+0 | 1+0 | 0+0 | | | | | |
| May 13-19 | 1+2 | 0+2 | 0+2 | 0+0 | | | | | | |
| July 15-21 | 3+2 | 1+1 | 1+1 | 1+1 | 0+0 | | | | | |
| Sept. 11-23 | 1+0 | 0+0 | | | | | | | | |
| Dec. 12-18 | 7+8 | 7(6)+7(6) | 0+3 | 0+1 | 0+1 | 0+0 | | | | |
| 1953 | | | | | | | | | | |
| Feb. 10-16 | 0+0 | | | | | | | | | |
| Apr. 16-22 | 5+2 | 3+1 | 1+1 | 0+1 | 0+1 | 0+1 | 0+0 | | | |
| June 11-17 | 16+15 | 11(10)+10 | 1+2 | 0+1 | 0+1 | 0+1 | 0+0[4] | | | |
| Aug. 14-20 | 7+6 | 0+0 | | | | | | | | |
| Oct. 27-Nov. 2 | 13+16 | 0+1 | 0+0 | | | | | | | |
| 1954 | | | | | | | | | | |
| Jan. 5-11 | 4+0 | 1+0 | 0+0 | | | | | | | |
| Mar. 9-15 | 0+0 | | | | | | | | | |
| May 14-20 | 5(4)+3 | | | | | | | | | |

[1] In each column the first figure represents males, the second females. Figures in parentheses show the number of mice released if this number was different from number captured.
[2] Skipped this period but was trapped in the next.
[3] One ♂ persisted through 19 periods.
[4] Assumed.

The periods were approximately 2 months apart. The interval usually was between 51 and 66 days; 4 times it was greater, 70, 74, 85, and 86 days. Dates of trapping are listed in Table I.

Traps were set near markers placed in a 60-foot grid as shown in Fig. 2. One trap was set at each site, not exactly at the marker, but at the nearest favorable location such as a fallen log, or the base of a tree or bush; a trap ordinarily was within 10 feet of its marker.

Traps were large-size (3 × 3 × 9-inch) Sherman box traps made of galvanized metal. Whole-kernel corn was used for bait and was the only bait after December 1950. Both peanuts and corn were used before this. Several different baits were tried in the first trapping period; corn was used alone for the first 3 days, peanut butter and oats were added on the 4th day, and corn and peanuts were used on the 5th, 6th and 7th days. The changes of bait did not seem to affect the mouse catch. Cotton nesting material was added to the traps during cold weather.

Traps were visited each morning, usually before 10 A.M., and were re-set then. Traps were left closed and in place between trapping periods. Mice were marked with numbered metal ear tags and released where trapped.

## Wood Mice

Wood mice (*Peromyscus leucopus*) were the most numerous mammals in the woodlot. The number trapped probably included very nearly all the resident mice that were adults or subadults. There are several reasons for believing this: (1) mice did not skip trapping periods; if a previously marked mouse failed to be caught

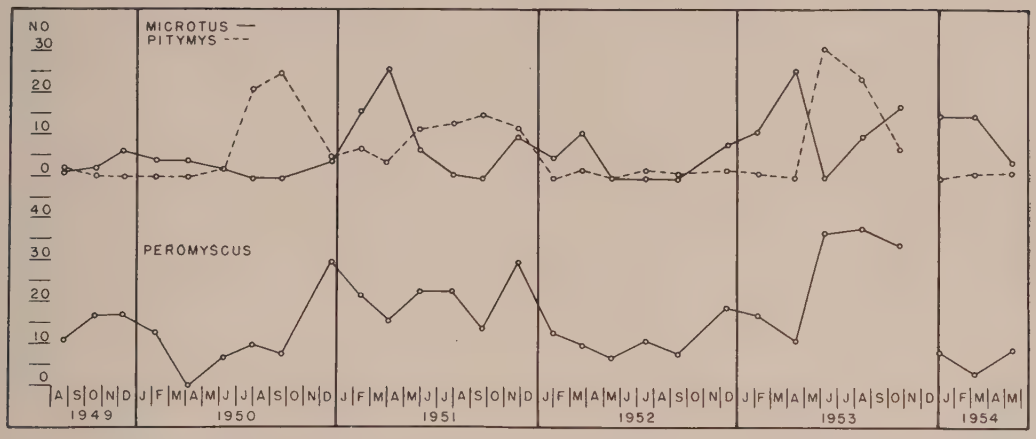
NO
MICROTUS —
PITYMYS ---
PEROMYSCUS
30
20
10
0
40
30
20
10
0
A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1949
1950
1951
1952
1953
1954

FIG. 4. Seasonal and annual trends of populations of Peromyscus, Microtus, and Pitymys, as indicated by total numbers trapped. The lines are interrupted in the latter part of 1953 because the regular November-December trapping period was omitted.

in a given period he was not trapped later, with but one exception; (2) mice that were caught in the woodlot in more than one period were trapped within the first 3 days of the 2nd and subsequent periods (except for one female not trapped until the 7th day); (3) mice normally traveled far enough that several traps were available in the range of each and mice were few enough that empty traps were available; (4) wood mice enter traps readily; an experimental study in a woods near the farm showed that all wood mice were trapped and marked within a week (Stickel 1946b).

Records of adults and subadults were considered together for most purposes, for, during the summer season, most of the mice were closely similar in age, and pelage characteristics of individuals changed rapidly. Small gray juveniles were excluded from the analysis. Very few of them were caught, and it seemed likely that the traps were not sensitive enough or set closely enough together to sample the juvenile population adequately.

### *Seasonal Changes*

The number of mice in the woodlot changed with the seasons (Figure 4 and Table II). It was highest in late fall (November-December), declined moderately in winter (January-February), and declined still farther in spring (March-April). The number increased during the summer (May-August), declined slightly in early fall (September-October), then increased again to the December high.

This seasonal pattern of numbers appeared each year, but deviations also were apparent. For example, (1) mice increased each summer, but in 1951 and 1953 the increase resulted in captures of nearly the same number of mice in early summer (May-June) as in late summer (July-August), whereas in 1950 and 1952, fewer mice were trapped in early summer than in late summer, (2) the usual early fall decline was not apparent in 1949; instead, the peak was reached in late October and maintained to December, (3) the population trend in 1953 was unusual in that a peak was reached in early summer and was maintained through the fall at approximately the same level; the customary early-fall decline was even smaller than usual. Although the woodlot was not trapped in November or December of 1953, it is unlikely that the population increased conspicuously beyond its October level, for the annual decline began early. Numbers dropped sharply by early January, whereas in other years the population stayed fairly high well into February.

The trend of numbers through the season was similar to that found by Burt (1940) in southern Michigan. He was able to relate the summer peak, the early fall dip, and the later fall peak to the times of emergence of young mice from their nests and their growth to independent activity. His area differed from ours in that his peak populations came a little earlier in the fall (October-November rather than November-December) and his low populations a little later in the spring (May rather than March-April). Snyder (1956) also found that peak numbers of wood mice were reached in October-November in southern Michigan.

A seasonal population trend from a low in spring to a high in fall as a result of spring and summer breeding is commonly referred to as the

TABLE II. Small mammals trapped in the woodlot 1949-1954*

| Period | Peromyscus | Microtus | Pitymys | Blarina | Sorex | Mus | Zapus |
|---|---|---|---|---|---|---|---|
| Aug. 23-29, 1949 | 11 | 1 | 2 | 14 | 0 | 8 | 3 |
| Oct. 19-25, 1948 | 17 | 2 | 0 | 4 | 0 | 15 | 0 |
| Dec. 13-19, 1949 | 17 | 6 | 0 | 3 | 0 | 11 | 0 |
| Feb. 8-14, 1950 | 13 | 4 | 0 | 0 | 0 | 2 | 0 |
| Apr. 4-10, 1950 | 0 | 4 | 0 | 0 | 0 | 8 | 0 |
| June 6-12, 1950 | 7 | 2 | 2 | 1 | 1 | 4 | 0 |
| Aug. 1-8, 1950 | 10(+2) | 0 | 21 | 2 | 0 | 5 | 2 |
| Sept. 21-27, 1950 | 8 | 0 | 25 | 5 | 0 | 9 | 1 |
| Dec. 15-21, 1950 | 30 | 4 | 5 | 0 | 0 | 8 | 0 |
| Feb. 13-19, 1951 | 22 | 16 | 7 | 1 | 0 | 0 | 0 |
| Apr. 5-11, 1951 | 16(+4) | 26 | 4 | 1 | 0 | 0 | 0 |
| June 1-7, 1951 | 23(+2) | 7 | 12 | 1 | 0 | 0 | 0 |
| Aug. 1-7, 1951 | 23 | 1 | 13 | 0 | 0 | 0 | 6 |
| Sept. 26-30, Oct. 1-2, 1951 | 14(+3) | 0 | 15 | 3 | 0 | 3 | 0 |
| Nov. 27-30, Dec. 1-3, 1951 | 30(+2) | 10 | 12 | 0 | 0 | 6 | 0 |
| Jan. 31, Feb. 1-6, 1952 | 14 | 5 | 0 | 1 | 0 | 0 | 0 |
| Mar. 21-27, 1952 | 10 | 11 | 2 | 0 | 0 | 0 | 4 |
| May 13-19, 1952 | 7(+1) | 0 | 0 | 0 | 0 | 1 | 0 |
| July 15-21, 1952 | 11(+1) | 0 | 2 | 0 | 0 | 3 | 2 |
| Sept. 11-23, 1952 | 8 | 0 | 1 | 4 | 0 | 0 | 0 |
| Dec. 12-18, 1952 | 19 | 8 | 2 | 3 | 0 | 0 | 0 |
| Feb. 10-16, 1953 | 17 | 11 | 1 | 2 | 0 | 0 | 0 |
| Apr. 16-22, 1953 | 11(+2) | 26 | 0 | 0 | 0 | 1 | 0 |
| June 11-17, 1953 | 37(+2) | 0 | 31 | 0 | 0 | 0 | 0 |
| Aug. 14-20, 1953 | 38 | 10 | 24 | 13 | 0 | 1 | 0 |
| Oct. 27-31, Nov. 1-2, 1953 | 34 | 17 | 7 | 6 | 0 | 6 | 1 |
| Jan. 5-11, 1954 | 8 | 15 | 0 | 3 | 1 | 1 | 0 |
| Mar. 9-15, 1954 | 3 | 15 | 1 | 3 | 0 | 0 | 0 |
| May 14-20, 1954 | 9 | 4 | 1 | 2 | 0 | 0 | 0 |

* Peromyscus numbers in parentheses indicate gray juveniles. Numbers for other species include individuals of all ages.

northern cycle. Fluctuations of woodland populations of *Peromyscus maniculatus* in New Brunswick (Morris 1955) are typical. Breeding began in spring and continued in summer, producing a population peak in August-September, after which numbers declined again. A similar pattern was found among *Peromyscus maniculatus* in a forested area in the Upper Peninsula of Michigan (Manville 1949). A population of *P. boylei* in the Sierra Nevada bred in spring and summer, reached peak numbers in July-August, then declined (Storer, Evans, and Palmer 1944).

The southern cycle differs. The population peak is in late winter or spring as the result of a breeding season that begins in the fall. There is little or no breeding in the summer, so the low point comes in late summer or early fall. The southern cycle was discussed by McCarley (1954) from his study of *P. gossypinus* in Texas, and from the work of others. Other work in the south has shown similar seasonal trends of Peromyscus numbers. For example: *P. nuttalli* in Florida (Pearson 1953), and in Texas (McCarley 1958); *P. polionotus* in Florida (Blair 1951), and in Georgia (Odum 1955); *P. leucopus* in Texas (McCarley 1954), and in Louisiana (Brooke Meanley unpublished).

Meanley trapped in an oak-hickory hardwoods in the Kisatchie National Forest, Rapides Parish. A line of 50 live traps was set for 3 days each month. Traps were 33 feet apart. His records show the following catch for 1955-56: Oct., 0; Nov., 0; Dec., 0; Jan., 4; Feb., 14; Mar., 14; Apr., 11; and May, 3.

Population trends of *P. leucopus* in southern Michigan and in Maryland, as shown by Burt's study and ours, must be considered intermediate. The peak of population in Maryland is reached in December, between the February-March peak described by McCarley (1954) for the southeast and the August-September peak of *P. maniculatus* in New Brunswick. The population trend in Maryland (and in Michigan) differs from both the typical northern and southern patterns in having a 2nd, lower peak in summer. This is a result of two peaks of breeding (spring and fall) although some breeding continues through the summer. An intermediate pattern closer to the northern type was followed by *P. maniculatus* in a wooded area in the Sierra Nevada (Storer, Evans, and Palmer 1944). Peak numbers were reached in July-August and in October-November, but, in contrast to our results in Maryland, the summer peak was the high one. *P. boylei* had a single summer peak in the same year, as noted earlier.

These generalizations concerning seasonal trends are useful for regional comparisons, but are not absolute. Striking variations and near-reversals can occur in a single area. The unusually early peak in the woodlot in 1953 is one example. Pearson (1953) reported an October peak for *P. gossypinus* in Florida in 1949, in contrast to late winter peaks reported by McCarley (1954) for the same species in Texas. Changes in the trend of numbers could be produced by any conditions of the environment that influence breeding (Pournelle 1952, Bissonette 1936: 383). Food and shelter often seem to be the critical factors. McCarley (1954) discovered a breeding colony of *P. gossypinus* at a grain and hay dump in August when there was no breeding by mice in the surrounding area. Bendell (1959) supplied food in excess on one of 2 islands in eastern Ontario and found that the main spring breeding of *P. leucopus* on the experimental island was a month earlier than on the control island where food was not provided artificially. In the north, where reproduction of mice ordinarily does not occur in the coldest months, breeding has been found where there was good shelter and an abundance of food (Linduska 1942). Jameson

(1953) believed that food was a basic determinant of fall breeding and subsequent numbers of *P. maniculatus* and *P. boylei* in the northern Sierra Nevada, California.

### *Yearly Changes*

The size of the Peromyscus population changed greatly from year to year (Figure 4 and Table II). Both 1951 and 1953 were good mouse years throughout. Populations were low through most of 1950 but the December peak was as high as in 1951. Relatively small numbers were trapped in 1952. Numbers also were low in 1949 and 1954, if they can be judged from the few trapping periods of those first and last years. Although both 1951 and 1953 were peak years, there were several differences between them. The peak number in 1953 was somewhat higher than that of 1951 and came earlier in the season despite a lower number in spring. In 1951, in contrast, a high population carried over from December of 1950 and numbers continued high throughout the year. There were differences in the low years also; the lowest point of any year was in April 1950, when no Peromyscus was trapped in the woodlot, but by December the population was high. The number of mice did not drop as low in April of 1952 but neither did it increase greatly by December.

In terms of population per acre, Peromyscus density at the seasonal peaks varied from 3.9 to 8.6 per acre. Seasonal lows varied from 0 to 3.6 per acre. Only at peak periods of peak years were densities as high as those of Peromyscus in wooded bottomlands areas of the center (Stickel 1946, 1948). But they were rarely as low as in a young, dry, upland oak woods where they numbered little more than one per acre in July 1946 (Stickel 1948).

Changes in numbers of mice in the woodlot were not entirely the result of local reproduction and mortality. The woodlot was far enough away from other woods and hedgerows that it is unlikely that individuals traveled back and forth regularly, but it was not far enough away to be isolated. The nearest wooded area was 500 feet distant. In other trapping studies on the farm, wood mice frequently were caught well out into fields when the weather was damp and nights were dark. Often they were caught at least as far from suitable habitat as the distance from the woodlot to other wooded areas. A few marked mice were known to travel to or from the woodlot. Their records are discussed later.

Peromyscus populations are known to fluctuate at intervals and sometimes the changes coincide with changes in food supply (Blair 1948, Jameson 1955). The importance of food was demonstrated strikingly in the experimental study made by Bendell (1959). The experimental island did not have a natural population of mice. An introduced population of 64 *P. leucopus* declined steadily, and none remained after a year. Wheat then was supplied continuously by automatic feeders and a new population of 20 mice was introduced. The mice survived and bred to a peak of 34 mice per acre, whereas the natural population on a control island nearby reached a peak of only 4 mice per acre in the same year.

Because of these results elsewhere, it seems most likely that food supply in the woodlot was important to production of peak populations in certain years. Our own data, however, are not complete enough to support this conclusion independently. There was a heavy crop of acorns and other mast on the refuge in the early fall of 1950, a year when Peromyscus numbers increased greatly from early fall to December and continued high into 1951. Pine-seed yield at the U. S. Forest Service Station, Beltsville, Maryland, also was high in 1950. In the high mouse year of 1951, acorns were plentiful again, but the pine-seed yield was light. In the low mouse year of 1952, we have no data for the oaks, but pine seed yield was low. The greatest peak of mouse numbers was in 1953. A very heavy yield of pine seed also was produced in this year. Pine seed fall does not begin until early November, however, whereas the mouse populations reached their peaks in early summer and had declined sharply by the end of December. Mouse numbers declined, therefore, during the very time when pine seed fall was heaviest. We do not have data for earlier-yielding fruit and seed crops for 1953 that might help explain the mouse increase in that year.

Changes in numbers of Peromyscus in the woodlot were not correlated with the crops in the surrounding fields; the crop pattern in 1950, a low mouse year, was the same as in 1953, a high mouse year. The border plantings apparently did not greatly influence the totals either, for the plantings did not fruit in 1951, the first high year. No correlations are readily apparent between mouse numbers and monthly averages of precipitation and temperature at the Beltsville Station, 5.5 miles west of the Refuge.

### *Sex Ratios*

Two hundred and fifty-one Peromyscus (adult or subadult) were captured in all the woodlot trapping from 1949 to 1954. There were 137

males and 114 females, a difference from a 50-50 ratio that is not statistically significant. Neither did the numbers of males and females differ significantly from each other within single trapping periods, as can be seen by inspection of Table I. Jackson (1952) found a primary sex ratio of 51.8% males among wood mice in southern New Jersey, which was not significantly different from a 50% ratio.

### *Reproduction*

Our field data permit only a general description of the annual breeding cycle of Peromyscus, for notes on breeding condition were not made each period. The breeding season began in early spring. Earliest records were for the trapping period of February 13-19, 1951, when all female mice were in oestrus or approaching it. The first spring-born young were caught April 9 and 10, 1951, and April 16 and 19, 1953. Breeding continued through the summer and early fall. Our records are not complete enough to show the proportion of the population that was breeding at any one time or to indicate changes in reproductive activity during this period. Breeding ceased during the winter. Seasonal reproductive patterns described by Jackson (1952) for wood mice in southern New Jersey probably are much the same as on the center. He did not determine the time when breeding began in the spring, but it was well underway by mid-May. He found that there were 2 peaks of breeding activity, one in late spring and another and higher one in August and early September. Pregnancy was reduced during July. Breeding continued until mid-October. *Peromyscus leucopus* began breeding in southern Michigan in mid-March (Burt 1940), about a month later than in Maryland. The breeding seasons of Peromyscus in other areas were discussed earlier in connection with seasonal population trends.

### *Length of Residence in the Woodlot*

The Peromyscus known to have lived in the woodlot longest was caught there in 19 consecutive trapping periods, a span of 38 months. This mouse, male 3348, was first trapped on December 15, 1950 and was last trapped on January 11, 1954. He was a subadult when first captured and so probably not more than 2 months old. (Snyder 1956, estimated that 1.5 months was the average age for mice during the post-juvenile molt.) By October of 1953 he had the grizzled appearance of an old animal. His may be record longevity for a wood mouse in the wild for it is greater than any of the records cited by Snyder (1956).

The next longest resident was male 3449. He was captured first on June 1, 1951 as a subadult and last on December 16, 1952, a period of 20 months. The female Peromyscus that lived in the woodlot longest was number 3359. She was captured first on December 15, 1950 as a subadult and last on March 21, 1952, a period of 18 months. Five other mice, one male and 4 females, were trapped in the woodlot during a full year. Histories of all wood mice trapped in the woodlot are shown in Table I.

A residence table was prepared to show the lengths of time that mice stayed in the woodlot and their expectancy of continued residence. The table was prepared by the method used for preparing life tables (Deevey 1947). The residence table was prepared directly from the field data shown in Table I; adjustments were made for mortality due to trapping. Data for the last trapping period were omitted. Another problem was considered in constructing the residence table. As data from all periods were to be combined, and the periods were not spaced exactly at 2-month intervals, it seemed that error might be introduced by the combination. For this reason special calculations were made to adjust the survival figures for each item to a base level of 60 days. The equation used is: Surviving number = Population at beginning $\times$ $(1\text{-}r)^n$, where $1\text{-}r$ = rate of survival (geometric), and $n$ = The number of 60-day units between the trapping periods. Tables constructed from these adjusted data were so nearly identical with those constructed from the raw data that the adjustment was considered to be an unnecessary complication, and the raw data were used instead.

Expectancy of residence for a newly-trapped mouse (adults and subadults combined) was about 3 months. Fewer than 5% remained in the woodlot for as long as 6 months. Fewer than half of the Peromyscus that were caught in the woodlot were trapped there in 2 or more trapping periods; the others were trapped in one period only. Table III shows these data and the expectancy of residence and proportion of mice remaining at successive periods of 2 months. The expectancy of residence of 3 months would indicate a minimum life expectancy of 4.5 months if mice were assumed to be an average of 1.5 months old at first capture. Actual life expectancy would be greater, both because the average age almost certainly was greater and because the records include disappearance as well as mortality. Blair

(1948) estimated that *P. leucopus* remained in his study plot an average of 4.6 months. *P. maniculatus bairdii* remained an average of 4.9 months. McCabe and Blanchard (1950) estimated an average life span of 5 months for *P. maniculatus gambelii,* 6 months for *P. truei,* and 9 months for *P. californicus.* All of these estimates concerned only mice that reached trappable age.

TABLE III. Residence table for Peromyscus and Microtus

| Period (2-mo. interval) | PEROMYSCUS MALES | | PEROMYSCUS FEMALES | | MICROTUS BOTH SEXES | |
|---|---|---|---|---|---|---|
| | Proportion remaining | Expectancy (months) | Proportion remaining | Expectancy (months) | Proportion remaining | Expectancy (months) |
| 1 | 1.000 | 2.92 | 1.000 | 2.80 | 1.000 | 1.74 |
| 2 | .477 | 3.04 | .436 | 3.14 | .240 | 2.08 |
| 3 | .189 | 4 14 | .232 | 3.00 | .123 | 0.98 |
| 4 | .082 | 6 24 | .081 | 4 76 | .007 | 1.00 |
| 5 | .041 | 9.48 | .071 | 3.28 | .000 | |
| 6 | .025 | 12.92 | .051 | 2.18 | | |
| 7 | .017 | 16 52 | .010 | 5.00 | | |
| 8 | .017 | 14.52 | .010 | 3.00 | | |
| 9 | .017 | 12.52 | .010 | 1.00 | | |
| 10 | .017 | 10.52 | .000 | | | |
| 11 | .009 | 17.00 | | | | |
| 12 | .009 | 15.00 | | | | |
| 13 | .009 | 13 00 | | | | |
| 14 | .009 | 11.00 | | | | |
| 15 | .009 | 9.00 | | | | |
| 16 | .009 | 7.00 | | | | |
| 17 | .009 | 5.00 | | | | |
| 18 | .009 | 3.00 | | | | |
| 19 | .009 | 1.00 | | | | |
| 20 | .000 | | | | | |

Snyder (1956), studying *Peromyscus leucopus* in southern Michigan, found that mortality accounted for a different proportion of the disappearances from his area in 2 winters. Life expectancies calculated at the different rates of the two winters were 26.5 weeks and 12.4 weeks (at 5 weeks of age). He found that disappearance rates, and so presumably also mortality rates, were essentially constant after 5 weeks of age. The average age of subadults at first capture was about 6 weeks. It seems satisfactory, therefore, to combine data from adults and subadults to estimate length of residence.

There appeared to be no consistent seasonal or annual trend in the proportion of mice that stayed in the woodlot from one month to the next. Numbers were small and variation was great, so there may have been too few data for a definite conclusion on this point. For example, 13 mice were released in February of 1950 and not one of them was caught again. In contrast, 7 mice were released in June of 1950 and 6 of them were captured again in August. The proportions of males and females that stayed in the woodlot from one month to the next were not significantly different.

### *Home Ranges*

Most Peromyscus that lived in the woodlot stayed in the same general parts of it from month to month. A few, however, seemed to shift their ranges from one month to the next; others traveled all over the woodlot in certain months, but stayed in a limited part of it in other months.

Home-range behavior and travels were studied from range maps made for each mouse in each period. Records of the 47 mice (23 males and 24 females) that were trapped in 3 or more trapping periods were considered in most detail.

To help compare the locations of ranges, centers of activity were calculated and distances between them were measured. The center of activity is a 2-dimensional average of the places of capture (Hayne 1949) and so is a useful indicator of the position of the home range. It is not intended to have other biological implications in the present study. Maximum distances between a mouse's centers of activity varied from 50 to 530 feet. The other distances are shown in Table IV. Position of the center of activity usually shifted back and forth from month to month, as shown in Figure 5a and 5b. Shifts of the center of activity usually were greater for mice with larger ranges, as would be expected. It is likely that apparent changes in position of the center of activity most often were the result of random variation, rather than an indication of actual changes of range. Some mice did change or shift their ranges, however, and these changes were reflected in distances between centers of activity that were greater than usual.

The maps of ranges and travels showed several patterns of mouse activity. We have grouped the variations into 4 categories for simplicity of description, even though some of them graded into each other. The groupings are somewhat arbitrary for the additional reason that we did not know the extent of travels of the mice when we were not trapping. It seems certain that at least some of them would have been assigned differently.

#### (1) *Stable ranges*

We judged from the maps that 79% of the mice (17 males, 20 females) had relatively stable ranges and stayed in the same general area from month to month. Typical examples are mapped in Figure 5a and 5b. The maps show the centers of activity for each month, and the places where the mice were trapped. The places of capture did not coincide exactly in any 2 months, especially at the edges of the ranges, but the ranges

TABLE IV. Travels of Peromyscus in the woodlot.

| Distances (feet) | Numbers of mice trapped in 3 or more periods that showed indicated maximum distances between centers of activity | | Numbers of Mice that Showed Indicated Maximum Distances Between Traps | | | |
|---|---|---|---|---|---|---|
| | | | Mice trapped 4 or more times in one week | | Mice trapped 14 or more times over-all | |
| | ♂♂ | ♀♀ | ♂♂ | ♀♀ | ♂♂ | ♀♀ |
| 0 | — | — | 3 | 5 | — | — |
| 1-60 | 1 | 6 | 14 | 12 | — | — |
| 61-120 | 6 | 8 | 35 | 41 | — | — |
| 121-180 | 6 | 3 | 49 | 33 | — | 3 |
| 181-240 | 1 | 4 | 37 | 22 | 2 | 6 |
| 241-300 | 3 | 1 | 23 | 9 | 7 | 5 |
| 301-360 | 2 | 1 | 12 | 1 | 4 | 3 |
| 361-420 | 0 | 0 | 7 | 0 | 1 | 1 |
| 421-480 | 2 | 1 | 1 | 0 | 3 | 0 |
| 481-540 | 2 | — | 4 | 2 | 2 | 1 |
| 541-600 | — | — | 1 | — | 4 | 1 |
| Average distances | | | 188.0 | 140.2 | 378.1 | 280.0 |

usually overlapped extensively; occasionally the captures of one month were more or less separated from those of the other months. These variations would be expected as a limitation of trapping, for the complete extent of a mouse's range scarcely could be shown by 7 captures (Stickel 1954). It is likely, also, that variations in the exact positions and boundaries of ranges did occur, and so were reflected in the trapping records.

(2) *Trip outside the home range.*

One mouse, female 2854, made at least 2 extended trips. She was trapped 36 times in 6 different trapping periods between June 7 of 1950 and April 11 of 1951. She was trapped 34 of these times on the northwest side of the woodlot in an area that was 360 feet across. The 2 other times, she was trapped on the opposite side of the woodlot: in April, she was caught in trap F-1, 480 feet from where she was caught the next day; in June, she was caught in trap B-1, 480 feet from the capture of the next day and 245 feet from the April capture. These 2 captures away from the usual range did not have much effect on the calculated positions of the centers of activity, which were only 254 feet apart.

(3) *Gradual shift of range*

Two mice shifted their ranges gradually across the woodlot. The best example was female 4121, who was trapped 30 times between June 12, 1953 and May 20, 1954. In June and August, her captures and centers of activity were in the north corner of the woodlot. In October, her captures extended across the mid-part of the northeast border. In January, March, and May, her captures and centers of activity were localized in the east corner and adjoining southeast side of the woodlot. The total distance was not great, but the progression was steady; the greatest distance between centers of activity was 432 feet, and the greatest distance between traps was 512 feet. Another mouse, male 3688, gradually shifted his range over a somewhat smaller distance.

(4) *Changing areas of use within more extensive ranges*

Seven mice apparently occupied different parts of the woodlot in different months. Certain of these shifted back and forth between different areas. The 2 females in this group, 1748 and 4052, used areas that were fairly close together. The 5 males (3391, 1612, 3449, 3844, and 3348) used areas that were farther apart. In addition, each of the males, except number 3391, traveled extensively over nearly the entire woodlot in at least one other trapping period. Their greatest travels were recorded in different months; 1612 traveled most widely in October, 3449 in September, and 3844 in both July and September. Number 3348 traveled most extensively in April, but also crossed the woodlot in May and in June. Any of the mice may have traveled widely at times that did not happen to coincide with periods of study. We have no certain explanation for their behavior. Perhaps the extensive travels were exploratory trips. It is possible also that a social hierarchy existed among the mice in the woodlot and that the more dominant mice ranged more widely than did those in subordinate positions, as Myers and Mykytowycz (1958) and Mykytowycz (1958) reported for rabbits (*Oryctolagus cuniculus*).

Part of the history of male 3348, one of the mice that appeared to range over the entire woodlot at some times and yet occupy limited portions of it at other times, is shown in Figure 5c. He was captured more often and over a longer time than any other animal in the woodlot: 118 captures in 19 trapping periods between December 15, 1950 and January 11, 1954. The map shows his capture sites for the entire study and the details for certain periods. He was trapped most frequently in the east quarter of the woodlot; records for 2 of these periods, April 1951 and August 1951, are shown on the map. He was trapped in the opposite quarter in 2 periods, December 1952 and February 1953, as shown on the map. His trap records for April 1953, in contrast, were widely distributed, and very nearly encompassed the records of all other periods combined. Capture sites for April 1953 are numbered in sequence on the map and con-

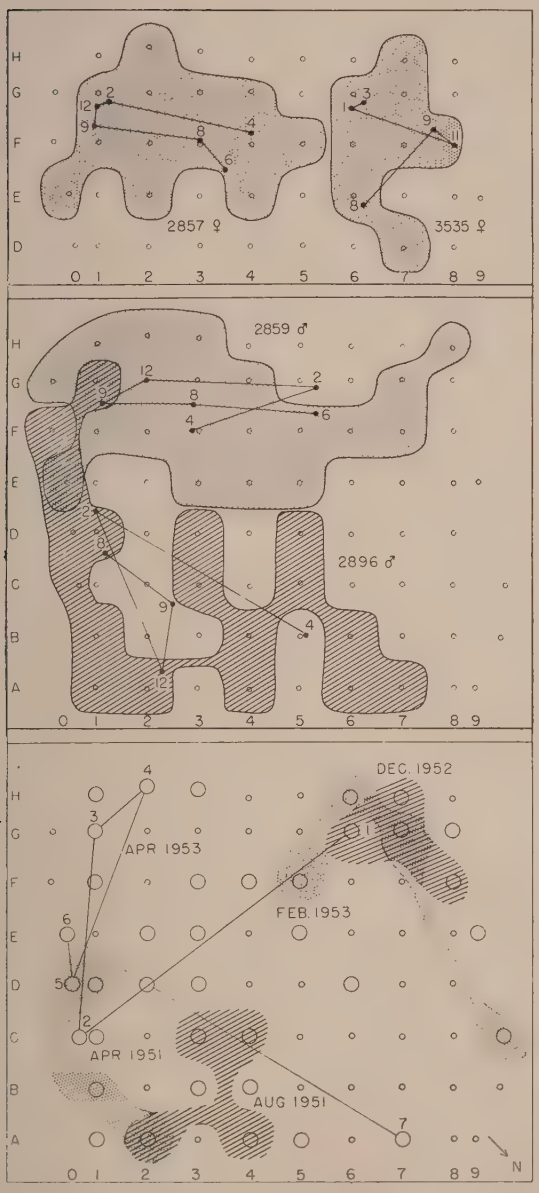


Fig. 5. a. (top) Typical long-term trap-revealed ranges of female Peromyscus. Number 2857 was trapped 35 times from June 10, 1950 to April 11, 1951. Number 3535 was trapped 22 times from August 1, 1951 to March 27, 1952. Centers of activity are shown as small solid circles that are connected by straight lines; numbers indicate the months.

b. (middle) Typical long-term trap-revealed ranges of male Peromyscus. Number 2896 was trapped 34 times from August 2, 1950 to April 11, 1951. Number 2859 was trapped 33 times from June 10, 1950 to April 11, 1951. Symbols as in 5a.

c. (bottom) Trapping history of male Peromyscus number 3348, who was taken 118 times from December 15, 1950 to January 11, 1954. Capture sites are shown as large open circles. Shaded areas show captures during certain single periods when he was trapped only in limited areas. These are typical of behavior in a number of other periods, as discussed in the text. Numbered trap sites connected by straight lines show sequence of captures in April, 1953, a period of extensive travel. There were 7 captures in each period shown.

nected with straight lines. The history of his trapping records can be summarized roughly as follows: December 1950, south corner; February and April 1951, east quarter; June 1951, diagonal route across woodlot; August, September, November, January 1951, east quarter; March 1952, east quarter, extending to south corner; May 1952, diagonal route across woodlot; July 1952, east quarter; September 1952, east quarter, extending to south corner; December 1952 and February 1953, west quarter; April 1953, almost complete circuit of the woodlot; June 1953, east quarter extending toward center of woodlot; October 1953, east quarter; January 1954, central area of 135 feet in traps where not caught before.

We do not know how fully the trapping records reflect the actual travels of the mouse. It seems safe to conclude, however, that the east quarter of the woodlot was occupied most frequently. He was caught most often in trap A2, 16 times in 7 different periods, including the 2 periods shown on the map. Other Peromyscus often were caught in this same trap when it was not occupied by number 3348. Peromyscus captures there totaled 85, making it the 3rd most-used trap. Most of the east section of the woodlot where number 3348 was caught so often was a preferred area for mice, as is discussed more fully later.

### *Size of Home Range*

Estimates of home-range size were made by comparing the travel distances recorded in a single trapping period with those recorded over a longer time.

A week's trapping was not enough to show the range size for most mice. Average distances increased with successive captures through the week. Individuals caught 4 or more times were trapped an average of only 2 times after the last known increase in range. Many of them (74 in 311 records) showed an increase at the final capture. Records of others were more complete, for 55 records showed 4 or 5 captures after the last known range increase. The effects of successive captures on known range size and the variation in the number of captures that may be necessary to show the complete range are discussed by Stickel (1954).

Weekly records were assembled first by months, but then combined when significant differences

were not found. There were relatively few records for each month, and we believe the data inadequate to show whether or not monthly differences existed. Trap-revealed travel distances within a week are shown in Table IV. Many mice are included in the tabulation more than once because of the combination of data from all periods. The average of the maximum distances between traps was 188 feet for males and 140 feet for females.

Trap-revealed ranges for a longer term were measured for the 43 Peromyscus trapped 14 or more times. These distances are shown in Table IV also. They average 378 feet for males and 280 feet for females. As home range is defined as the area that an animal uses in the course of his regular day-to-day activities, these long-term ranges should not be called home ranges. The distances are increased by shifts in range from month to month as well as by the various occassional travels discussed above. Estimated sizes of long-term ranges are more reliable than those of weekly ranges. Average distances at successive captures increased steadily until the 9th capture (females) and 10th capture (males), then began to level off. Subsequent increases in the averages were relatively small. Individuals averaged 6-7 captures after the last known range increase. Fourteen mice were trapped 10 or more times after the last increase. Only 5 increased their recorded ranges at the final captures. In all, there were 1051 captures of the 43 individuals.

Average travel distances over the long term almost certainly are greater than distances across the true home range, and the average distances during a week surely are smaller. The average home range (expressed as minimum range length) thus probably was between 200 and 400 feet for males and between 150 and 300 feet for females. These distances are roughly the same as those estimated for Peromyscus in an upland oak area on the center and greater than those estimated in in the bottomland (Stickel 1946a, 1948, 1954).

### *Dispersal*

A few mice that were trapped in the woodlot also were trapped elsewhere. Two were captured in dwellings; 3 others were taken in other trapping programs on the farm.

(1) Male 1770, subadult, trapped in the woodlot once only, August 27, 1949. Caught again December 22, 1949 in a snap trap in the basement of a building a little more than ½ mile west.

(2) Male 3985, subadult on December 12, 1952, trapped in the woodlot December 12, 17, 18, 1952 and February 10-16, 1953. Caught again April 19, 1953 in basement of dwelling approximately 950 feet east.

(3) Female 2943, gray juvenile when trapped in marshy meadow on May 31, 1950. Caught June 6-12, 1950 in the woodlot, 1550 feet away.

(4) Female 4270, juvenile, trapped August 26 and 27, 1953 in multiflora rose hedge. Caught in woodlot October 28, 30, 31, 1953, about 460 feet away.

(5) Female 4397, adult, pregnant, trapped September 11, 1953 in shrubby border of woods. Caught in woodlot October 27-30, 1953, about 1570 feet away.

The first 4 records probably represent the normal dispersal of young animals from their birthplaces. The 5th may indicate a change of home range.

### *Distribution in the Woodlot*

Although wood mice were caught in every trap in the woodlot at one time or another, they were caught much more frequently in some traps than in others. In order to find if mouse distribution correlated with the vegetative pattern, a map was prepared to show the number of mouse captures at the different sites. The comparisons are shown in Figure 2.

Deciduous areas were favorable for trapping mice. Captures were especially numerous in the traps of the southeast border zone along the old fencerow (II and IIa). Dense ground cover of honeysuckle or mixed brushy growth, and oak trees of fair size all may have helped to make the area suitable for mice. The mixed deciduous area around the spring (I) also was a center for mouse captures, as was the north corner zone (Ia). Both of these areas had much dense and tangled undergrowth as well as trees of fair size. Few wood mice were caught in the parts of the west marginal zone (Ic) that were grassy or herbaceous.

The number of mice captured in the pine zones seemed to depend on the nature of the undergrowth. Trapping was especially good in zone IV and IVa, where deciduous undergrowth was dense. Most of the other pine-dominated areas were relatively unfavorable for mice; these also were areas where undergrowth was sparse. Area IIIb was relatively unfavorable despite a heavy ground cover of honeysuckle.

More captures were made around the margins of the woodlot than in the interior. The reason appeared to be that the interior contained fewer

deciduous areas and less dense undergrowth. Traps set in deciduous zones in the interior were as successful as marginal traps. All marginal traps, moreover, were not equally successful. Trap-success was poor along the parts of the southwest border that were dominated by pine or by very young deciduous growth. As the border became more dense by natural succession during the years of trapping, trap-success improved somewhat. This is shown by the fact that traps H-3 to H-7 (6.8% of the traps of the woodlot) made 2.7% of the Peromyscus captures in 1949, 1.4% in 1950, 1.4% in 1951, 3.6% in 1952, and 5.4% in 1953.

During the early years of trapping, trap-success also was poor along the pine-dominated northeast border, but improved so much that there were more captures for all the years together than we would have expected from the appearance of the woods. Traps A-3 to A-7 made 1.7% of the mouse captures in 1949, 2.0% in 1950, 5.1% in 1951, 7.4% in 1952, and 7.8% in 1953. This margin of the woods was bordered by a *Lespedeza bicolor* planting and the mouse traps were set at the edge, nearly in the border. The growth of the hedge to dominance and fruiting presumably was the reason for the increased number of captures.

Even within the more favorable areas, where mice were caught frequently, certain traps were much more successful than others. Often it was possible to recognize the reasons. Four traps made more than 80 captures apiece: A-2 was in a tangle of honeysuckle and dead branches on a little mound at the base of a willow oak; G-1 was underneath a tent-like tangle of honeysuckle at the base of a small sweetgum that stood near the edge of the gully; G-6 was in young deciduous growth not far from the base of the large old sour gum that overlooked the spring. In contrast, trap F-8, although it was in an area of dense young deciduous growth, did not appear to be more favorably located than neighboring traps where fewer mice were caught. Trap F-5 made 63 captures despite being in a pine-dominated area; the reason apparently was that it was very close to brushy deciduous areas and also was set in a sheltered spot under the bases of a group of small pines that had fallen over nearly to the ground. Variations in cover type or density or special local conditions at trap sites probably explain most of the variation in captures per trap, although proximity to mouse nests, sensitivity of individual traps, or chance alone may sometimes have been important.

The importance of ground cover to Peromyscus has been shown in other studies. Morris (1955) caught more *P. maniculatus* in forest areas where vegetation, debris, or slash was present than where the forest floor was mainly bare needle litter. Smith (1959) caught most *P. leucopus* in coniferous planting with considerable herbaceous undergrowth.

### Meadow Voles

Meadow voles (*Microtus pennsylvanicus*) were trapped regularly along the margins of the woodlot except in summer. They presumably included parts of the adjoining shrub borders and fields in their ranges. Although some of the traps were set in the midst of honeysuckle or other cover, none was set in a runway and no special effort was made to catch Microtus. Traps also were set farther apart than they would have been for a study of Microtus. For these reasons, the Microtus that were trapped probably did not include all that were present. Data seem adequate to give some information on fluctuations in numbers, length of time individuals stayed in the woodlot, travels, and habitat preferences.

#### *Numbers and Fluctuations*

Seasonal and annual fluctuations of Microtus are shown in Figure 4. Peak numbers were trapped in 1951 and 1953; the number trapped in 1954 was only a little lower. Small numbers were trapped in 1950, intermediate numbers in 1952.

Seasonal population peaks came in April of the years of highest density, 1950-51 and 1952-53. In these years the number of Microtus caught in the woodlot increased rapidly during the winter. In the other years numbers increased from September-October to November-December, then remained about the same through the winter and into April. Numbers declined after April each year to a summer low. The low period continued through the summer and into early fall except in 1953. In this one year, numbers increased in the summer, from June to August and from August to October.

Increase in numbers of Microtus in the woodlot in fall and winter seemed to be the result of invasion from surrounding areas. Departure to more favorable breeding habitat in spring probably accounted for a large part of the spring decline. It is unlikely that any important part of the increase in numbers during winter was the result of new voles being born there, for breeding was not prevalent during winter. Probably very few litters were born after October. Breeding did not always cease completely, however, for young were born in a trap in another area of the

farm on February 25, 1950, and we suspected that young were born to one female in the woodlot in February, 1953.

Seasonal trends of numbers and reproduction in a more favorable habitat were studied in 1949-50 (Stickel, unpublished). Live traps were set in a 5-acre field of winter wheat (which grew up in hay after the wheat harvest) and in an adjoining marshy meadow. This area was about 400 yards from the woodlot. General reproductive activity of Microtus evidently began in March and April, for half of the voles trapped in the first period, May 25-31, were juveniles. A period of reduced breeding followed in early summer before widespread breeding was resumed. Breeding continued into fall producing a population peak in October. Numbers then declined through the winter, during which there was little or no breeding. Unfavorable winter conditions were reflected also in curtailed growth of young voles. Three juveniles that were trapped in October or November were still of juvenile size some months later. One was trapped last in March, one in February, and one in January. A subadult trapped in November was still of subadult size in January. Similar cessation of growth was reported for *Microtus ochrogaster* in Kansas (Martin 1956). Total monthly captures in the field and meadow area on the center were: May, 33; June, 23; July, 21; August, 67; September, 50; October, 121; November, 35; January, 15; February, 11; March, 12; April, 9; May, 11.

This spring-to-fall trend of reproduction and population increase is similar to that described by Hamilton (1937) for New York, except that his peak populations usually were reached in September instead of October. He reported winter breeding and later peaks during years of highest populations. Linduska (1950) found, in contrast, that winter reproduction and increase was the usual pattern in an upland farm area in Michigan. He reported a seasonal trend of abundance that was closely similar to the pattern we found in the woodlot. Peak numbers in his study were in January-February, somewhat earlier than in ours. Reasons for the trend were somewhat different in his area from in ours, however, because his populations of Microtus were augmented by winter breeding. He concluded that Microtus that appeared in September and October probably were invaders from wet grassland but that "the subsequent high populations of fall and winter resulted from multiplication in the uplands and not from a mass population shift."

Annual changes in Microtus numbers that produced peak populations in 1951 and 1953 are not easy to interpret. Low numbers in the woodlot did not necessarily reflect low numbers elsewhere, for many Microtus were caught in the field and meadow in the fall of 1949, a year when they were scarce in the woodlot. It would seem reasonable to suppose, however, that high numbers in the woodlot must mean high numbers elsewhere, particularly as the years 1951 and 1953 also were favorable for Peromyscus and Pitymys. This conclusion is not certain, however, for the peaks could have been produced by progressively unfavorable changes in the environment elsewhere that caused more voles to move to the woodlot as winter progressed. Because of these uncertainties, we consider our data unsuitable for interpretation in terms of cyclic highs and lows.

### *Length of Residence*

About 24% (35 of 146) of the Microtus that were trapped and released in the woodlot were trapped there again in later months. About 10% (14) were trapped in 3 trapping periods. Only one was trapped in 4 trapping periods; female 3382 was trapped first on December 17, 1950, as a subadult, and was trapped last on June 7, 1951—a period of nearly 6 months. The expectancy of residence of Microtus in the woodlot was calculated as for Peromyscus (Table III). The individual expectancy was 1.7 months at the first trapping period, 2.1 months at the 2nd trapping period, and 1.0 month at the 3rd trapping period.

The number of voles that remained in the woodlot long enough to be caught in more than one trapping period varied from month to month. For example, all 3 voles released in December 1950 were caught again not only in February 1951 but also in April; one was caught again in June. In contrast, not one of the 8 voles released in August of 1953 was recaptured. Known survival from period to period at the different seasons is shown in Table V. Voles released in December or February were most likely to be taken again. Voles released in April were much less likely to be recaptured. The small numbers of voles captured in other months makes it difficult to evaluate their chances of recapture. The numbers in the table include all the voles for each period, not just the ones captured for the first time. For this reason, some voles are included more than once and the total numbers are greater than the total number of individual voles.

Length of life of Microtus could not be estimated from the woodlot data. Residence there probably had little relationship to actual life span.

TABLE V. Known survival of Microtus from period to period at different seasons.*

| Date of Period 1 | Periods | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1949 | | 1950 | | 1951 | | 1952 | | 1953 | | 1954 | |
| | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 | 1 | 2 |
| Jan.-Feb. | — | — | 4 | 1 | 16 | 10 | 9 | 4 | 10 | 6 | 14 | 7 |
| Mar.-Apr. | — | — | 3 | 0 | 25 | 2 | 11 | 0 | 26 | 2 | 14 | 0 |
| May-June | — | — | 1 | 0 | 7 | 0 | 0 | 0 | 2 | 2 | — | — |
| July-Aug. | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 8 | 0 | — | — |
| Sept.-Oct. | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 17 | 3 | — | — |
| Nov.-Dec. | 5 | 2 | 3 | 3 | 10 | 5 | 8 | 4 | — | — | — | — |

* Mice that died in traps are excluded and mice that skipped trapping periods are included; numbers differ, therefore, from those in Figure 4.

Others have found that few Microtus live as long as one year (Hamilton 1937). Blair (1948) reported that Microtus remained in his plots an average of 4.2 months. Martin (1956) recaptured 3 *Microtus ochrogaster* after 611 to 624 days, but most other individuals were trapped over a period of less than a year. The number of *M. ochrogaster* that was known to live as long as a month varied from about 40% for June to nearly 80% for November and December; individuals born in autumn seemed to have the greatest life expectancy.

### *Home Range and Travels*

Most of the 35 meadow voles that were trapped in more than one month were trapped in the same area each time. Twenty-one voles were trapped in at least one of the same traps each period. For 6 others the trap sites in the different periods were separated by 60 feet or less. The distances were between 60 and 120 feet for 3 voles and between 120 and 180 feet for 5 voles. It is possible that some of the greater distances may represent range shifts. Most of the voles that remained in the woodlot apparently continued to live in the same home ranges.

Data concerning the travels of the voles within a trapping period were limited by the small number of recaptures, which may have been at least partly the fault of the trap spacing. The traps may have been so far apart that no trap was present in the range of some of the voles; for others there may have been only a single trap available. Only 30 Microtus were trapped as often as 4 times in a single period. The greatest distances they traveled between traps were: 0 feet (4 voles), 1-60 feet (15 voles), 61-120 feet (5 voles), 121-180 feet (5 voles), 407 feet (1 vole). These figures may represent the travels of only the more wide-ranging individuals and so probably are not a fair sample of the travels of the majority of the population.

The vole that traveled 407 feet was male 3991, an adult. He was trapped at A-8 and A-9 for 6 days, December 12-17. Then on the 18th he was taken on the opposite side of the woodlot, at H-7. He was not trapped again. A smaller trip was made by female 4717. She was trapped once in January 1954 at C-8. In March, the next period, she was trapped first in F-5, next back in C-8, a distance of 255 feet.

### *Distribution in the Woodlot*

Meadow voles were trapped around the edges of the woodlot in places where cover was at least moderately dense. Greatest numbers were caught in areas II, Ia, and Ic (Figure 3). Area II, where dense honeysuckle covered the ground, and area Ia, where there was dense ground cover of mixed kinds, also were good areas for wood mice. Area Ic, however, was in an earlier grassy and herbaceous stage that was favorable for Microtus but not for Peromyscus. Many Microtus but few Peromyscus were trapped in A-9, which was in a little grassy open area. Undergrowth in the vicinity of trap C-9 was a dense tangle of vines. The trap at this site caught many Microtus, and Peromyscus and Pitymys as well, even though the overstory was pine. Meadow voles were caught only occasionally in pine-dominated areas where there was little ground cover. Few places in the woodlot resembled the grassy-sod or moist-meadow habitats where Microtus usually are found, so it seems natural that the woodlot was abandoned in summer. The presence of Microtus in the woodlot at any season is evidence of their remarkable versatility and sensitivity to environmental changes that has been noted by others (Bailey 1924, Hamilton 1940).

## PINE VOLES

Pine voles (*Pitymys pinetorum*) lived in the woodlot and were caught there during many of the trapping periods. Their numbers were sampled in a very limited way, however, for the traps were set on the surface of the ground instead of in or near the underground runways of the voles.

Very few Pitymys were trapped in 1949 or in 1952; higher numbers were caught in 1950, 1951, and 1953, although the peak number in 1951 was lower than the peaks in the other 2 years (Figure 4). Large numbers of both Peromyscus and Microtus also were caught in 1951 and 1953. Seasonal changes in numbers of pine voles that were trapped may not be a true indication of population changes. They may have spent more time above ground and entered traps more readily at some seasons than at others. The peaks in captures

were in summer, from June to September, and the low periods were in winter. Peaks of population may have come at the same time as the peaks in trapping success, but it seems unlikely that the trapping records are a completely satisfactory reflection of actual population changes through the seasons. Benton (1955) stated that "There is some evidence that above-ground daytime activity varies with the season, but further data are needed to establish seasonal trends."

The average length of time that pine voles stayed in the woodlot cannot be estimated from the trapping data, for many voles lost their ear tags and could not be identified when re-trapped. Twenty-five pine voles retained their tags long enough to be identified in 2 or more months. The longest record was for male 3528; he was trapped first on June 7, 1951, and was trapped for the last time on July 17, 1952, a period of a little more than 14 months. Two other Pitymys were trapped over a period of approximately 8 months; another was trapped over a period of a little more than 5 months. Six voles were trapped in 3 different periods (about 4 months) and 15 were trapped in 2 different periods (about 2 months).

Pine voles that were trapped in more than one month usually were in or near the same traps each time. Seven voles were caught in at least one of the same traps in each month; for 8 voles the capture sites in the different months were within 60 feet of each other; for 6 voles they were between 61 and 120 feet; and for 4 voles they were between 121 and 180 feet.

Travels of voles within a trapping period were restricted also. There are 16 records of pine voles being trapped as often as 4 times in a single month. Four of these were caught always in the same trap. The greatest distances recorded for the others were: 1-60 feet (4 voles), 61-120 feet (6 voles), 190 feet (1 vole), and 255 feet (1 vole).

Pine voles were caught in both pine and deciduous areas as shown in Figure 6. Captures were much less frequent in the pine areas, however, particularly those in the interior of the woodlot. Some of the most favorable areas were the same as for Peromyscus and Microtus. The old hedgerow and honeysuckle zone of the southeast margin was popular, as were certain traps in other places. Pitymys differed from Peromyscus in having proportionally fewer captures in the moister deciduous zone around the spring and more along the southwest edge, where it was caught fairly often even in traps in the pine area.

Pitymys in other areas live in a wide range of habitats, although they are taken in moist places least often (Benton 1955). We have trapped substantial numbers of them in the bottomland forest of the refuge. They live in the terrace and upland woods also, in the old apple orchard, in fields and hedgerows, and in the privet (*Ligustrum* sp.) and japonica (*Chaenomeles* sp.) plantings near dwellings.

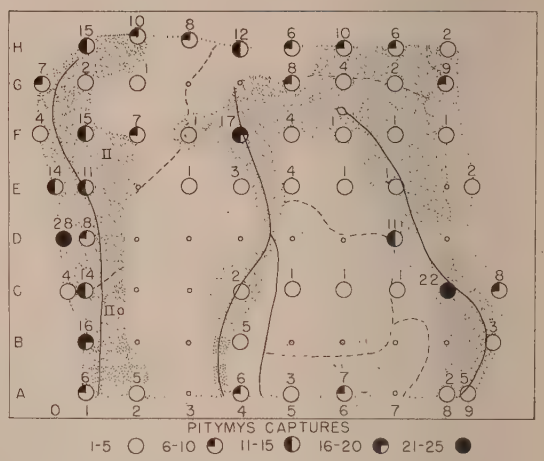


FIG. 6. Map showing distribution of Pitymys in the woodlot. Numerals and large circles at the trap sites show the total numbers of captures, 1949-54. Other symbols as in Figure 2.

## House Mice

Some house mice (*Mus musculus*) were trapped along the margins of the woodlot. They apparently lived in the surrounding fields and entered the woodlot borders only occasionally, for few were caught more than once or twice in a trapping period and only 3 were trapped in more than a single month. Four mice were trapped 4 or more times in a period; one of these traveled 204 feet along the edge of the woodlot, one was caught in a single trap each time, and the 2 others were trapped in places 66 feet and 132 feet apart. Of the 3 mice that were trapped in at least 2 periods, the longest record is for female 2802. She was trapped first on December 16, 1949 and last on June 12, 1950, a period of about 6 months. One mouse was trapped over a period of 2 months, and one over a period of 4 months. Two of the mice that were trapped in different periods visited a single trap each time. The other one visited traps that were 60 feet apart.

More house mice were trapped in 1949 and 1950 than in later years (Table II). Their decrease after 1950 may have been caused by changes in the vegetation at the edges of the woods, where the cover became more dense each year. The decrease also could have reflected a decline in the number of house mice in the fields.

### Other Species

Small mammals of a few other species were trapped in the woodlot. Their numbers are shown in Table II.

*Blarina brevicauda.* Short-tailed shrews were trapped occasionally each year, but most of them died in the traps. The few that were released alive were not marked. They were trapped in the interior of the woodlot as well as on its borders.

*Sorex cinereus.* Two specimens were trapped. They may not have been as scarce as this suggests, for most of the traps were not set lightly enough to capture them.

*Zapus hudsonius.* Jumping mice probably were not regular residents of the woodlot; they were recorded in only 7 trapping periods. Only 3 individuals were trapped more than once, and 2 of these traveled the full length of the woodlot between captures. None was caught in more than a single period.

*Tamias striatus.* One chipmunk was trapped twice in the woodlot in August, 1951.

*Mustela frenata.* A weasel was caught in August, 1950. It entered 3 different traps and killed a mouse in at least one.

### Summary

Small-mammal populations of a 4.4-acre farm woodlot on the Patuxent Research Center, Maryland were studied by periodic live trapping for nearly 5 years, 1949-54. The woodlot is a mixed stand of pine and deciduous trees, most of which began to grow in an abandoned farm field in the decade 1914-24. Traps were set in a 60-foot grid at intervals of approximately 2 months. *Peromyscus leucopus, Microtus pennsylvanicus,* and *Pitymys pinetorum* were the principal species.

Peromyscus were most numerous. They fluctuated seasonally from a high in December to a low in April. Numbers increased to a low midsummer peak, declined slightly, then increased again to the high for the year in December. Seasonal trends in the numbers were intermediate between seasonal cycles in the north and those in the south. They were similar to the pattern in Michigan, although population peaks in fall were about a month later in Maryland. Our December populations varied from 3.9 to 8.6 Peromyscus per acre, April populations from 0 to 3.6 per acre. High numbers were present through most of 1951 and 1953. One Peromyscus was trapped in the woodlot for a period of 38 months, and several others for a year or more. The average expectancy of residence was about 3 months. No seasonal differences in persistence in the woodlot were noted. Most Peromyscus maintained home ranges in the same general area from month to month. A few made trips away from their usual ranges, or gradually shifted their ranges. Several mice ranged over the entire woodlot at some times, but occupied more limited parts of it at other times. The history of the travels of a mouse that lived there 38 months is discussed in detail. The greatest distance between capture sites was taken as an indication of range size. Distances, measured for mice trapped 14 or more times apiece, averaged 280 feet for females, 378 feet for males. These were long-term records and so included any shifts of range or trips that occurred. True home ranges almost certainly were smaller. Captures in a single week were too few to show actual ranges, but the average figures can be taken as a minimum; averages for mice taken 4-7 times in one week were 140 feet for females, 188 feet for males. True home-range sizes can be considered to lie between the weekly and the long-term figures. Peromyscus preferred the deciduous parts of the woodlot. Dense ground cover of viny tangles, honeysuckle, or shrubs was important, for areas of this type were heavily used wherever they occurred, even if beneath an overstory of pine. Use of the northeast border of the woodlot increased through the years as a *Lespedeza bicolor* planting grew to fruiting size.

Microtus used the honeysuckle, grassy, and tangled zones of the woodlot borders as winter habitat. In most years their numbers increased from few or none in summer to a low peak in December and remained about the same until April, when they declined sharply. In 1951 and 1953, numbers increased steadily into April, apparently as a result of continued movement to the woodlot from surrounding areas. Numbers declined in April as usual. Individual Microtus had an expectancy of residence of less than 2 months. One stayed 6 months. While there, they maintained home ranges in limited areas.

Pitymys were trapped most commonly around the margins of the woodlot, but also were taken in the interior in both pine and deciduous areas. Peak captures were in the June-September period, perhaps because of peak abundance then, but perhaps, instead, because of more activity above ground at that season. Peak numbers were trapped in 1950, 1951, and 1953. Most Pitymys that were trapped more than once were trapped in the same limited areas each time.

Other species that were trapped occasionally included *Mus musculus, Blarina brevicauda, Sorex*

*cinereus, Zapus hudsonius, Tamias striatus,* and *Mustela frenata.*

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# METABOLISM OF AN ANTARCTIC FISH AND THE PHENOMENON OF COLD ADAPTATION[1]

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## INTRODUCTION

The purpose of this study is to compare the metabolic level of an antarctic fish adapted at temperatures of —2° to 0°C to the metabolic levels of several species from tropical to arctic, and from warm eurythermal to cold stenothermal, environments.

When fish and many other poikilotherms *adapted* normally to moderate and high temperatures are *acclimated* to a given low temperature, their metabolism tends to drop to a level below that of species normally adapted to the given low temperature. The comparatively high metabolism of the cold adapted forms is known as "cold adaptation." In terms of oxygen consumption rates, Scholander *et al.* (1953) note that oxygen consumption by tropical fishes at 30° is about 5 times the rate for arctic species at 0° compared to 30-40 times the hypothetical rate of tropical forms at 0°.

The physiological explanation of cold adaptation is not well understood although there are many published references on the subject as indicated in the reviews of Bullock (1955) and Fry (1958). While activity may be involved, it should be pointed out that both active and sedentary fishes occur in most environments regardless of temperature. If the metabolic level of the arctic fishes, which are adapted to seasonal temperatures from —2° to 0° up to 10° to 15°, is displaced upward from tropical and temperate species, then an antarctic species continuously adapted to ice-cold temperatures should have its metabolic level at comparative temperatures displaced upward even more.

Unfortunately there are few year-long field studies of fish metabolism which make comparisons of seasonal changes in metabolic levels possible. According to data from Wohlschlag and Juliano (1959), metabolic levels of the warm temperate bluegill (*Lepomis macrochirus*) vary from the 0° standard level (Krogh 1916) in winter up to the 30° tropical level (Scholander *et al.* 1953) in summer. From various sources of data presented by Fry (1957), it is apparent that normal metabolic levels of fish usually lie somewhere between these two extremes. For this reason a comparison of seasonal metabolic changes for species ranging from warm eurythermal to cold stenothermal environments should be useful in interpreting the ecological significance of cold adaptation.

The logistic support provided by the U. S. Antarctic Research Program and the U. S. Naval Task Force 43 during Operation Deep Freeze IV and the aid of Messrs. John H. Dearborn and Hugh H. DeWitt in carrying out the field studies are gratefully acknowledged.

## MATERIALS AND METHODS

The nototheniid fish, *Trematomus bernacchii,* a benthic species used in this investigation, occurs in the vicinity of McMurdo Sound (77° 51′ S. — 166° 38′ E.). The range of *T. bernacchii* is around the Antarctic continent and as far north as the South Orkney and South Shetland Islands (Norman 1940). Throughout this range, sea surface temperatures are generally below 0° (U. S. Navy 1957). At McMurdo Sound, adjacent to the Ross Ice Shelf, the fish live continuously under a heavy sea ice cover, except for only a few weeks in some summers.

The specimens for the metabolism determinations were taken by traps set through the ice at 10-90-meter depths, except for one specimen taken by hook and line. The $0_2$ contents of the sea waters were near saturation and the temperatures were uniformly near —1.86°. Fish were transported to a hut within one hour of capture and kept in a large aerated aquarium immersed in a sea ice bath. The ice bath and aquarium temperatures could be maintained within 0.1° by controlling the amount of ice in the bath. All fish were studied at normal environmental salinities of approximately 34.5 o/oo. Oxygen consumption rate determinations at —1.9° to —1.0° were made after several hours acclimation to the selected temperature; at temperatures from —1.0° to +1.5° temperatures were increased about 0.1° per hour and maintained at the desired level for about 12 hours prior to $0_2$ consumption determinations.

The method of determination of the oxygen uptake rates involved the use of the 10.4-liter circular chamber described by Wohlschlag (1957).

[1] This study was supported by National Science Foundation Grant NSF-G-6328.

Initial $O_2$ concentrations within the chamber were at saturation and the oxygen content declined to no less than about 75-80% of saturation at the end of 60- or 45-minute runs during which there were 4 or 5 determinations of the chamber $O_2$ content. A least-squares regression calculation of the decline of $O_2$ within the chamber with time gave a direct rate of oxygen consumption for each of the 27 fish studied. The weight range was from 18 to 325 g and the temperature range from —2.0° to +1.5°. Swimming velocities were not measurable because the thigmotactic response of this species to the sides and bottom of the moving chamber was greater than their rheotactic response to the moving water. Hence oxygen consumption rates were determined for resting fish only.

Data have been analyzed by the regression method used by Wohlschlag (1957) and by Wohlschlag and Juliano (1959), as well as by the conventional "metabolism-temperature curve" method.

## Results

The relationships of the oxygen consumption rates per unit weight (metabolism) and temperature are shown in Figure 1. When compared to similar laboratory or field studies over such wide weight and narrow temperature ranges these data are not unusually variable, except, perhaps for the several observations discussed below.

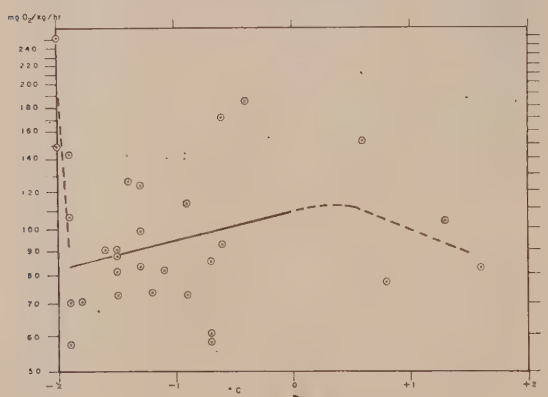


FIG. 1. *Trematomus bernacchii* metabolism-temperature plot. Solid line has slope of 0.060 log mgs $O_2$ consumed per hr per kg for each degree centigrade increase in temperature. Broken lines indicate possible deviations from linearity at temperature extremes.

Two of these fish were inadvertently cooled from —1.86° to —2.00° at which temperature they were held for 6 and 7 hours, respectively, before the one-hour metabolism run. Both individuals remained nearly motionless. Since both specimens could be made to swim rather vigorously for 5-10 consecutive minutes after each run, it was concluded that they were not adversely affected by the excessive cooling even though their oxygen consumption rates (Fig. 1) appear high. Because these 2 rates are high and there was no way to make suitable studies of the effects of excessive cooling, the 2 values are connected with the main body of the Figure 1 data by a broken line.

Within the —1.9° to +1.5° range there appears one technical difficulty associated with short-term acclimation at the higher temperatures. The 12-hour acclimation period at temperatures above —1.0° is probably inadequate to prevent a tendency for suppressing the oxygen consumption rates of the four fish above 0° as shown by the Figure 1 broken line. The least-squares slope of 0.060 (solid line) appears to be a realistic coefficient of increase in log oxygen consumed per unit weight for each degree rise in temperature between —1.9° and +0.4°. Several of the relatively low values in the middle temperature range are possibly due to the fact that these fish were unavoidably warmed slightly during the short period when they were taken from the traps to the colder holding aquarium. The single hook-and-line caught fish was warmed to +0.4° and cooled to —0.7°. The higher values are inexplicable; spontaneous activity would not account for them.

Multiple regression treatment is possible in the form:

$$\hat{Y} = a + b_w X_w + b_t X_t,$$

where $\hat{Y}$ is the log mgs $O_2$ consumed per hour, where the independent variables are respectively $X_w$, log body weight in grams, and $X_t$, temperature in degrees centigrade, and where the partial regression coefficients are respectively $b_w$, log mgs $O_2$ consumed per hour for each log unit increase in body weight, and $b_t$, log mgs $O_2$ consumed per hour for each degree increase in temperature.

For 27 determinations (excluding the two —2.00° results), the equation rounded to 4 decimal places is:

$$Y = -0.5104 + 0.7520\, X_w + 0.0382\, X_t.$$

For this equation the overall multiple correlation is 0.92 ($P < 0.001$) with a standard error of estimate of 0.1109, the weight partial regression coefficient is highly significant ($P < 0.001$) with a standard error of estimate of 0.0651, and the temperature partial regression coefficient is not significant ($P \sim 0.2$) with a standard error of estimate of 0.0300.

Since there appears a tendency for the oxygen consumption rates of the 4 fish above zero degrees to decline, and since the one hook-caught

fish may have a depressed oxygen consumption rate, the equation omitting these along with the —2.00° determinations becomes:

$$\hat{Y} = -0.5731 + 0.7881\,X_w + 0.0498\,X_t$$

based on a total on 22 fish. Even with the loss of the additional 5 degrees of freedom, the overall multiple correlation is 0.93 ($P < 0.001$) with a standard error of estimate of 0.1136, the weight partial regression coefficient is still highly significant ($P < 0.001$) with a standard error of estimate of 0.0730, and the temperature partial regression coefficient is "improved" but still short of significance ($P \sim 0.1$) with a standard error of estimate of 0.0339.

The results of these 22 determinations raised

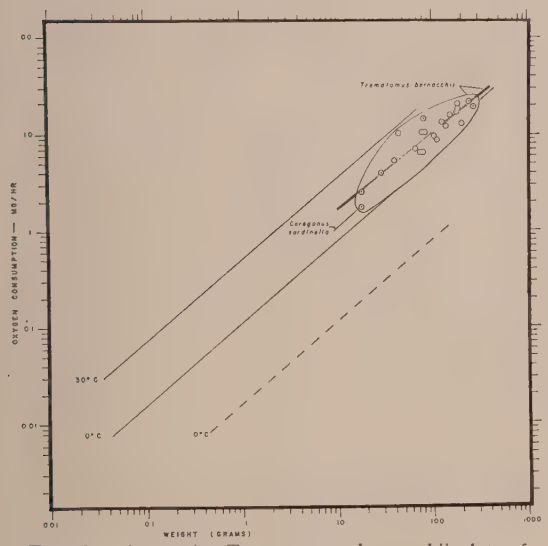


FIG. 2. Antarctic *Trematomus bernacchii* data for oxygen consumption rate and body weight relationships at 0°C with comparisons to other arctic and tropical data (see text).

to 0° are plotted in Figure 2 as a regression of oxygen consumption per hour and body weight. In the same Figure are also the regressions from Scholander *et al.* (1953) showing comparable relationships for tropical species at 30°, for arctic species at 0°, and for tropical species extrapolated by Krogh's (1916) normal curves to 0°. The Figure 2 *Coregonus sardinella* summertime data (Wohlschlag 1957) are based on the equation:

$$\hat{Y} = -0.8687 + 0.8910\,X_w + 0.0138\,X_t + 0.0243\,X_s$$

in which the notations are the same as above, but with the addition of the coefficient for swimming velocity $X_s$. These data are reduced to zero swimming velocity and to 0° to indicate that the method of measuring $O_2$ consumption rates used in this study compares favorably with that of Scholander, *et al.* and that their zero-degree arctic line can be extended for heavier fish. The *C. sardinella* line probably would coincide even more closely, but for the rather low 0.0138 temperature coefficient used to reduce the data from the 8.3° to 10.8° range to 0°.

## DISCUSSION

### *Metabolic Characteristics of* T. bernacchii

The data of Figure 1 indicate rather definitely that the antarctic *Trematomus bernacchii* tends to show a decline in metabolic rate with temperatures above those which the species would experience in nature. Whether this or other antarctic species could eventually be artificially acclimated to temperatures much above zero upon prolonged retention in aquaria is not known, but from the data of Scholander *et al.* (1953) it is fairly certain that the arctic species not only are naturally adapted to far greater temperature ranges than *T. bernacchii,* they too exhibit a metabolic decline when laboratory acclimation temperatures rise above maximum environmental temperatures of 10-15°. On this basis *T. bernacchii* is adapted to about the lowest possible temperature and is extremely stenothermal.

From Figure 2 oxygen consumption rate-weight relationships, *T. bernacchii* appears to be even more displaced upward than the 4 arctic species at 0° studied by Scholander *et al.* and the single arctic species studied by Wohlschlag (1957). Thus the phenomenon of metabolic cold adaptation for *T. bernacchii* is real to the extent that the oxygen consumption-weight relationship for 0° (Fig. 2) is displaced upward midway between the 0° arctic and the 30° tropical data of Scholander *et al.* (At —1.86° the relationship is but slightly below the 0° *T. bernacchii* line and well above the 0° arctic line).

### *Attentuation of Metabolic Ranges*

This conclusion suggests that there should be a progressive upward displacement of 0° oxygen consumption levels as adaptations for different species progress from warm to cold waters. Accordingly, it is instructive to investigate the extremes of metabolic levels of various fishes naturally adapted to a seasonal range of temperatures and to investigate the average temperatures and metabolic levels of progressively cold adapted species to seasonal growth. Warmest environments would be experienced by stenothermal tropical species and coldest by stenothermal polar species such as *T. bernacchii* at the freezing temperature of sea water. Eurythermal species of intermediate temperate environments would be

adapted to a range of temperatures lying between these extremes. The extreme levels of metabolism to be discussed are of the order of the 30° line (Fig. 2) for tropical species and the normal, or standard, 0° line as the minimum hypothetical level for fishes which are not cold adapted.

While data from various laboratories are not always given in terms of absolute values of oxygen consumption rates and individual weights of fish, weight ranges are often limited, distinctions between "standard" and "resting" metabolism are not always made, techniques are varied, acclimation regimes are not standardized or often collated with environmental temperatures, and while there may be considerable diversity among metabolic rates of different species in the same waters, it is nevertheless possible to illustrate in a broad, general, way some phenomena associated with metabolism at natural temperature extremes.

For warm non-freezing temperate freshwater environments with temperatures ranging seasonally from, say, 5° to 30°, the seasonal metabolic ranges are broad. The $0_2$ consumption-weight relationship at zero activity and at 30° for the bluegill (*Lepomis macrochirus*) on the basis of summer data is a line which lies slightly above the 30° tropical line (Fig. 2); the corresponding line at 5° based on winter data is a line which lies near the 0° hypothetical tropical, or Krogh's standard, line (data from Wohlschlag and Juliano 1959). At 30° the metabolic relationship for the goldfish (*Carassius auratus*) is slightly above the 30° tropical line and at 5° it is near the 0° standard line (data from Fry and Hart 1948, which Basu 1959 notes are slightly lower than those of other workers). For the brown bullhead (*Ameiurus nebulosus*) from the northern portion of its range, both the 30° and 5° metabolic relationships appear to be above the respective 30° and 0° lines of Figure 2, although the range between 5° and 30° is approximately of the same order as the ranges for the bluegill and goldfish (data for single specimen from Paul and Fry, in Fry 1947). Although comparable data at lower temperatures are unavailable, the carp (*Cyprinus carpio*) at 30° has a metabolic level equivalent to the 30° tropical line (data of Oya and Kimata, in Basu 1959). These data indicate that seasonal metabolic ranges of eurythermal warm water species cover the approximate range from the tropical 30° level to the standard 0° level illustrated by Scholander *et al.* and reproduced in Figure 2.

For cooler temperate waters which freeze in winter and which have a temperature range from 4°, or even 0°, up to 20°-25° in shallow waters, the seasonal metabolic range appears to be narrower than for warm temperate species. Over a range of about 5° to 20-25° comparative metabolic data are available from Job (1955) for speckled trout (*Salvelinus fontinalis*), from Gibson and Fry (1954) for lake trout (*Salvelinus namaycush*), from various unpublished sources in Fry (1957) for goldeye (*Amphiodon alosoides*), for yellow perch (*Perca flavescens*) and for brown trout (*Salmo fario*). For all these species the oxygen consumption-weight relationships extrapolated to 0° would be well above the standard 0° line, but below the 0° arctic line; the corresponding relationships at about 20°-23° correspond approximately to the 30° tropical line. The maximum temperatures normally tolerated by these species are also about 20°-23°.

Seasonal temperature ranges in arctic fresh waters would ordinarily be between 0+° in winter to as much as 15°-20° in summer and in marine waters would be from about −2° to about 10°. From the data of Scholander *et al.* (1953) for the stickleback (*Pungitius pungitius*), the blackfish (*Dallia pectoralis*), the polar cod (*Boreogadus saida*), and the sculpin (*Myoxocephalus quadricornis*) as well as from the data of Wohlschlag (1957) for the whitefish or riapushka (*Coregonus sardinella*), it appears that the 0° arctic line of Figure 2 is a realistic average of 0° metabolic levels for cold adapted fish. For these arctic data at normal summer temperatures the corresponding metabolic levels would be near the 30° tropical levels, except in the case of the sticklebacks where $Q_{10}$ values appear to be quite high. Thus the oxygen consumption rates corresponding to the 30° line would be at about 15° for the blackfish, 10° for the polar cod and sculpin, and at about 10° for the whitefish in marine waters; since the temperature coefficient for the whitefish in fresh waters is low, as mentioned above, their metabolic level at, say, 15° would be slightly below the 30° line.

From these published data it would appear that the upper metabolic limit at upper environmental temperature limits is of the same order for tropical, warm eurythermal, cool eurythermal, and nearly stenothermal arctic species, while the metabolic levels at the lower environmental temperature limits tend to increase with cold adaptation. Thus, with respect to seasonal metabolic *ranges*, there appears a progressive "cold adaptational attenuation" with the greatest range for warm eurythermal species and the minimum range for polar stenothermal species.

Even without average environmental tempera-

ture data for some of the above species, it appears reasonable to suppose that the *average* annual metabolic levels for different species would range approximately from the 30° level of Figure 2 for tropical stenotherms down to a level somewhat above the arctic 0° level—a level typified by the stenothermal antarctic *Trematomus bernacchii* at —1.8° to —1.9°.

Because the relationship between laboratory and natural temperatures is not often specified in the physiological literature, the metabolism data of temperate marine species reviewed, *e.g.*, by Fry (1957, 1958) will not be discussed here, although these data fit into the above scheme in a general way. However, note that marine species are usually more stenothermal than freshwater species, even if laboratory acclimation over a broad temperature range is possible as shown by Scholander *et al.* for their tropical species.

### *Implications*

With the metabolic level of *Trematomus bernacchii* as an indication of the total metabolism at about the lowest continuous temperature to which fishes are adapted, 2 provocative questions may be posed as a stimulus to further theoretical and applied ecological studies of fish production rates. The first question involves the relative proportion of total metabolic energy utilized for growth. For example, Olsen's (1955) data on growth at very active South Georgian chaenichthyid species, which lack blood pigment, indicate that at sea surface temperatures of about —1° to +2° these species grow faster than, say, northern Alaskan *Coregonus sardinella* at temperatures from 0° to 10° (Cohen 1954); the relatively sluggish *T. bernacchii* at about —1.8° to —1.9° has about the same annual growth rate as *C. sardinella* (in preparation). The question is: Is there a possibility of an increased efficiency of energy conversion into growth from warmer to polar waters in the same sense that there is cold adaptation? The 2nd question involves the fact, pointed up by Scholander *et al.* that an upper metabolic level at around 30° is about 30-40 times greater than the lower level at 0° which is pertinent to warm temperate species in winter. If the mechanisms of regulating metabolism were known, could they be manipulated artificially to raise the metabolic level (and growth) of a warm temperate species at winter temperatures to the correspondingly higher metabolic levels of polar species at the same temperatures?

## Summary

1. Metabolic characteristics were determined for *Trematomus bernacchii*, which is an antarctic benthic species living at year-round temperatures of —1.8° to 1.9°C. Metabolism was measured on the basis of oxygen uptake rates of fish confined to a closed chamber.

2. Oxygen consumption rates increased with temperature from —1.9° up to about 0°; the rates tended to decrease with temperature increases above 0°. The species is thus quite stenothermal.

3. The log mgs $O_2$ consumed per hour ($\hat{Y}$) can be related to log body weight in grams ($X_w$) and to temperature in degrees centigrade ($X_t$) as follows:

$$\hat{Y} = -0.5731 + 0.7881\, X_w + 0.0498\, X_t.$$

4. At 0° the metabolic level of *T. bernacchii* is higher than arctic forms at the same temperature. This fact verifies and extends the principle of cold adaptation.

5. From a comparison of selected data on metabolism of warm eurythermal through cold stenothermal species, there appears to be an attenuation of the seasonal metabolic range as species are progressively cold adapted. The metabolic range attentuation occurs by virtue of the increase in metabolic levels at the lower natural environmental temperatures due to cold adaptation and by virtue of the retention of the same general upper level at upper environmental temperatures even though these maxima decline from warm to polar environments.

6. Questions are raised as to the possibility that polar species may have a greater efficiency of energy conversion into growth and to the possibility that the mechanisms of cold adaptational control of metabolism may be applied to increase the growth of warm eurythermal species at low temperatures.

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# SPORADIC MASS SHOREWARD MIGRATIONS OF DEMERSAL FISH AND CRUSTACEANS IN MOBILE BAY, ALABAMA[1]

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At infrequent intervals in Mobile Bay, crabs, shrimp, and several species of fish crowd to the shallow water where they may be easily taken by anyone on the beach at the time. This phenomenon, locally termed "Jubilee," has heretofore been unreported in literature.

Sporadic mortalities of demersal fish and crustaceans are common in various parts of the world. Periodic mortalities of fish have been reported in the Walvis region of South Africa (Copenhagen 1953) and in the Bay of Concepcion in Chile (Falke 1950). At both of these locations the mortalities occur under specified meteorologic and oceanographic conditions, abetted by the geography of the region concerned. In the Chesapeake Bay there are frequent mortalities of blue crabs held in crab pots in deeper water during summer months. These mortalities have been attributed to lack of oxygen (Beaven 1958). Carpenter and Cargo (1957) report more than 25% mortality in blue crabs held in pots in water above 28°C and with oxygen concentration less than 0.6 ml/l.

In Mobile Bay, however, mortalities seldom occur. Fish and crustaceans rarely approach a moribund state and after several hours they swim off. The theory has been advanced that these shoreward migrations (hereafter called "jubilees") occur when certain meteorological and oceanographic factors are in coincidence. A discussion of this theory follows.

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## History of Jubilee

Most jubilees occur within a 12-mile shoreline on Mobile Bay extending from Daphne south to just below Point Clear. This area is crowded by "summer homes" and several commercial fishermen base their operations here on a year-round basis. Captain Frank Phillips, a commercial fisherman and lifelong resident of this area, states that he has observed jubilees for about 60 years and that his father had also seen jubilees during all of his life. He indicates that neither frequency nor intensity of the jubilees has changed during these years and that, though differences may be noted from year to year, the general trend has not shown any variation. Other long-time residents of the area corroborate this.

Interviews with a number of people who had seen many jubilees revealed the following concurring observations:

1. Jubilees occur only in summer.
2. They usually occur in early morning hours, *i.e.*, before sunrise.
3. The wind on the day previous and during the jubilee is from some easterly direction. If wind direction changes, the jubilee will cease.
4. There is a rising tide during a jubilee; a change to falling will stop the jubilee.
5. There are 2 water masses meeting, with the saltier water invading during a jubilee.

There was a difference of opinion as to whether or not local rains might produce a jubilee.

From 1946 to 1956 inclusive, 35 such occur-

rences have been reported in Mobile Bay, varying from none in 1954 to 10 in 1950 (Table I).

TABLE I. Frequency of jubilee by year and by month.

| Date | No. of Jubilees |
|---|---|
| 1946 | 1 |
| 1947 | 2 |
| 1948 | 2 |
| 1949 | 1 |
| 1950 | 10 |
| 1951 | 2 |
| 1952 | 6 |
| 1953 | 4 |
| 1954 | 0 |
| 1955 | 6 |
| 1956 | 1 |
| June | 8 |
| July | 3 |
| August | 21 |
| September | 5 |

They have been reported in June, July, August, and September, with 21 of the 35 occurring in August. Thirty-three of the 35 were reported from the eastern shore; 2 from the western shore.

The Mobile Press-Register has an active interest in the jubilee phenomenon and maintains a clipping file on the subject dating to 1946. Since summer homes in the jubilee area are at about 100-foot intervals and the occupants keep an active lookout for jubilees, it can be assumed that nearly every occurrence during this 11-year period was reported. Furthermore, many of these houses are occupied on a year-round basis, especially in the Fairhope and Daphne area, assuring the detection of out-of-season jubilees.

The following excerpts from stories in the Mobile Press-Register illustrate the magnitude of some jubilees:

6-16-47: An estimated 1000 persons gathered on the beach . . . many caught as many as 100 flounders.

8-7-50: One family backed a pickup truck to the beach and tossed flounders and crabs into the vehicle. By 3 AM they had nabbed about 125 flounders, also plenty crab.

9-18-50: One group got 70 flounder, a tubfull of softshells (blue crab) and a boatload of hardshells. They scooped up the hardshells to get them out of the way as they were on top of the softshells and flounders.

## Description of Bay

Austin (1954) described Mobile Bay as follows: "Mobile Bay has an overall area of approximately 297.18 square miles (nautical), averages 9.81 feet in depth at mean low water and attains a maximum depth of 60 feet off Fort Morgan near the main Gulf entrance to the bay. The bay is 27 nautical miles in length, 19.8 nautical miles at its widest point, and averages 11 miles in width over its entire length."

In general, the bay runs north and south. At the north the Mobile, Tensaw, Appalachee and Blakley Rivers enter the bay; of these the Mobile and Tensaw are the most important in terms of river flow and accompanying sediments.

The chart of flood tide surface currents (Figure 1) is a reproduction of a figure used by Austin (1954). This chart is based on 170 current measurements over a period of 6 days in October 1952. Personal observations throughout the year support the pattern as plotted.

The jubilee phenomenon occurs most frequently along the upper eastern shore of the bay from Point Clear to just above Daphne. They occur occasionally south of Point Clear to Mullet Point and on the western shore at Deer River and Dog River Point. The Point Clear to Daphne area is characterized by a near shore bluff ranging from a few feet to about 100 feet in height. Water deeper than 10 feet is found as near shore as 150 feet, which is the maximum beach slope in the upper part of the bay. Surface salinity in this area is from 1 to 15 o/oo during summer months.

## Physical and Meteorological Conditions Attendant to Jubilees

*Time:* The history of jubilees prior to 1953 was taken from newspapers and the time was not always recorded. In the years 1953-1956 every jubilee occurred during dark hours. Ten of the 11 were after midnight and before sunrise. The duration varied from one to 6 hours, and one in 1952 continued all night. Residents report "about 2 hours" as average.

*Extent:* Most jubilees are quite limited in breadth. Newspaper stories usually describe it as "500 feet" or "a quarter of a mile" in a certain vicinity. One in 1956 affected 5 miles of beach, and this was termed "biggest by far in many years." It is usually reported that the larger the physical dimensions the more intense is the jubilee.

On 2 occasions jubilees were reported at 2 locations on the same night, in each case about 8 miles apart. Both times, the more southern jubilee was reported as being small.

*Tide:* Thirty-two of the 35 jubilees occurred during a time of predicted (from U. S. Coast & Geodetic Survey Tide Tables) rising tides. One occurred on a falling tide and 2 began on a rising tide and continued on a falling tide.

Observers state that a change of tide usually signals the end of the jubilee.

*Wind:* The data on wind direction given in

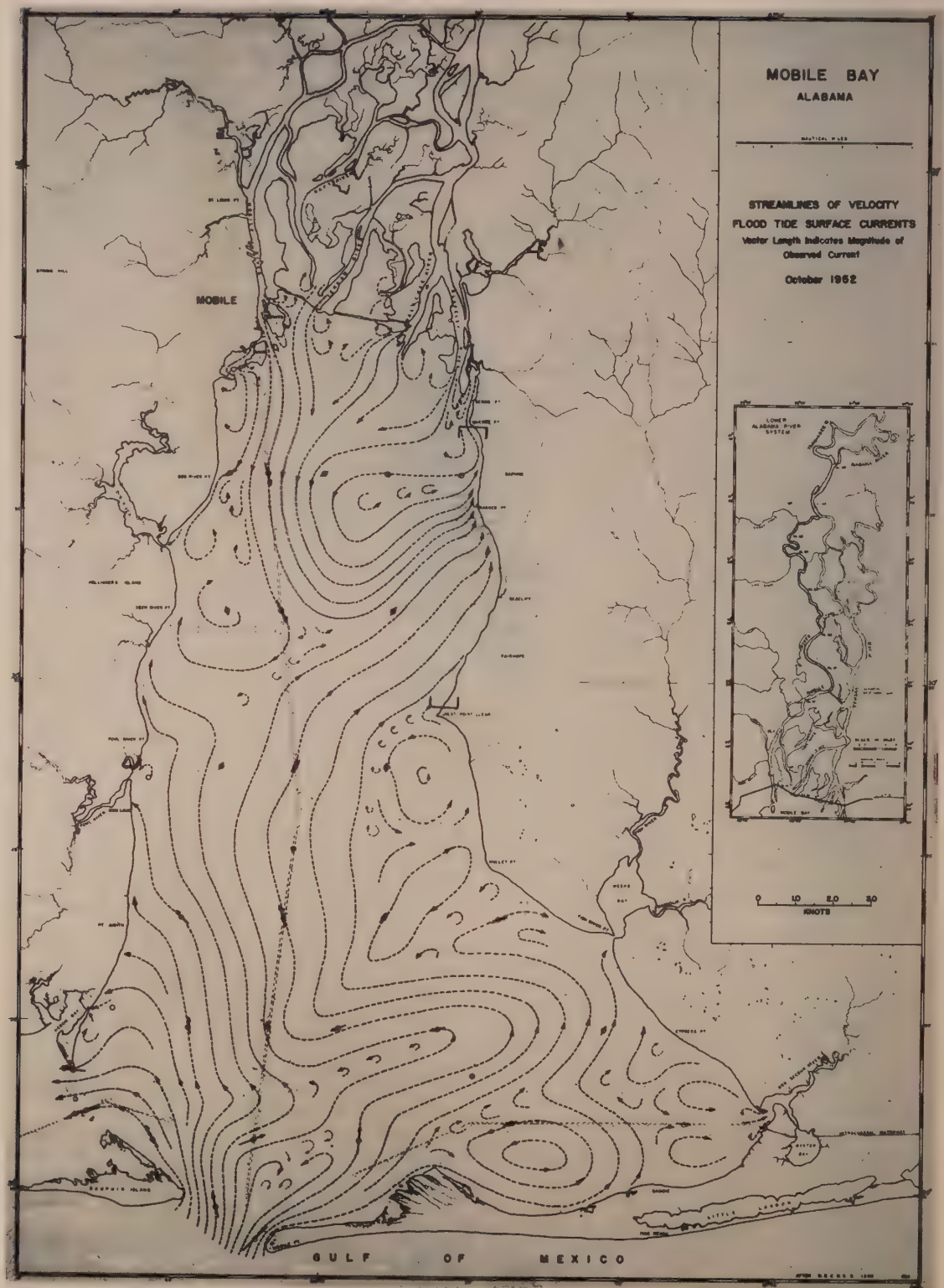


FIG. 1. Flood Tide Surface Currents in Mobile Bay. Most jubilees occur in the area bracketed along the upper eastern shore. Note the converging inshore currents in this area.

Table II were taken from records at the Bates Field Weather Station, located on the northwest corner of the bay, about 5 miles inland. Only the data concerning dates of jubilees on the Eastern shore are included.

Table II. Wind direction in relation to jubilees.

| Wind Direction | Occurrence on day before jubilee | Occurrence at time of jubilee |
|---|---|---|
| NW | 1 | 3 |
| N | 20 | 12 |
| NE | 5 | 5 |
| E | 5 | 11 |
| SE | 1 | 0 |
| S | 0 | 1 |
| SW | 1 | 0 |
| W | 0 | 1 |

Since the distance between this weather station and the Daphne area is 15 miles, wind conditions could be expected to vary because of the land-water mass relationship (diurnal monsoon effect), especially in the absence of a strong pressure system, in which case the wind blows from land to water at night and from water to land during the day. Daphne is on the east shore and Bates Field on the northwest of Mobile Bay, and differences in wind direction are common. As the wind blows toward the water at night, when the wind direction is north at Bates Field it is likely to be east on the eastern shore of the bay.

Observers are unanimous in reporting an east, northeast, or southeast wind on the day preceding and at the time of the jubilee.

*Rain:* Local rainfall was checked at the Fairhope and Bay Minette stations and no correlation could be found. During 1954, the year of no jubilees, the local annual rainfall was the lowest of any of the 11 years; however, below normal precipitation was recorded in 1950 also, and 10 jubilees occurred that year.

Using only data for the summer months, the most rain was recorded in 1949, during which time there was one jubilee. The driest summer was 1952 when 6 jubilees occurred, and the next driest was 1954 when none occurred.

## Chemical Observations

To facilitate chemical observations, a water testing apparatus was constructed following Swingle (1953). This permitted $O_2$ and $CO_2$ observations in the field.

It was found extremely difficult to obtain chemical observations during the course of a jubilee for several reasons. First, the short duration of a jubilee was made even briefer by the hour's drive from my home on the western shore. Second, the area of beach affected was so limited that many escaped all my sparsely spaced informers. Third, the local telephone exchange operator was a rather sound sleeper.

Just following a jubilee on the morning of August 16, 1955, water samples were checked in the vicinity. The first samples were taken along the public wharf in Daphne between 6 and 7 AM. At this time the salinity varied from 2.7 o/oo in 6 inches of water to 10.7 o/oo in 4½ ft of water. The sampling locations were less than 100 feet apart. The oxygen found at the deeper location was 0.35 ml/l; that at the shallower location was not checked but, in 3 feet of water along the same wharf, the $O_2$ was 1.05 ml/l. About 3 hours later a sample was taken at this latter location; the water was 5.1 o/oo salinity and 3.40 ml/l $O_2$. These data are presented in Table III.

Table III. Observations following a jubilee at Daphne. August 16, 1955—Jubilee lasted until about 0500.

| Location | Time | Depth Ft. | Temp. °C | Sal. 0/00 | $O_2$ ml/l | $CO_2$ ml/l |
|---|---|---|---|---|---|---|
| Daphne Warf | 0615 | ½ | — | 2.7 | — | — |
| " | — | 3 | 28.5 | 5.0 | 1.05 | 4.20 |
| " | 0630 | 4½ | 27.5 | 10.7 | 0.35 | 4.48 |
| " | 0645 | 2½ | — | 7.2 | 1.58 | 3.92 |
| " | 1020 | 4½ | 29.5 | 6.6 | 1.75 | 3.50 |
| " | 1000 | 3 | 29.0 | 5.1 | 3.40 | 1.96 |
| Villa Mercy | 0715 | 0 | 27.5 | 3.7 | — | — |
| about 6 ft. | — | 2 | 29.0 | 6.4 | 1.50 | 7.00 |
| from shore | 0745 | 0 | 27.0 | 4.3 | — | — |
| " | — | 2 | 29.0 | 7.9 | 1.40 | |
| " | 0810 | 0 | 28.0 | — | 2.59 | 4.06 |

At the Villa Mercy station, about ½ mile north of the Daphne wharf, top and bottom water samples were taken in water 2 feet deep. The salinity of the bottom water was nearly twice the salinity of the top water (Table III). Oxygen was checked only at the botom.

On July 28, 1955, conditions were reported to be "right" for a jubilee. A check of the water at about 2 feet revealed the following:

| Time | Salinity | Oxygen ml/l | $CO_2$ ml/l |
|---|---|---|---|
| 2200 | 6.5 o/oo | 2.8 ml/l | 10.56 |
| 2245 | 5.4 o/oo | 4.2 ml/l | 5.60 |

Wind had changed from east at 2200 to a strong southwest at about 2220, and the jubilee did not materialize.

On the morning of July 12, 1957 a jubilee occurred in the vicinity of Daphne. On the afternoon of July 12 water samples were checked at a station 2 miles offshore of Daphne. The results are given in Table IV. There was a sharp gradient of oxygen: 6.44 ml/l at the surface, 4.97 ml/l at 6 feet, and 0.38 ml/l at 9 feet

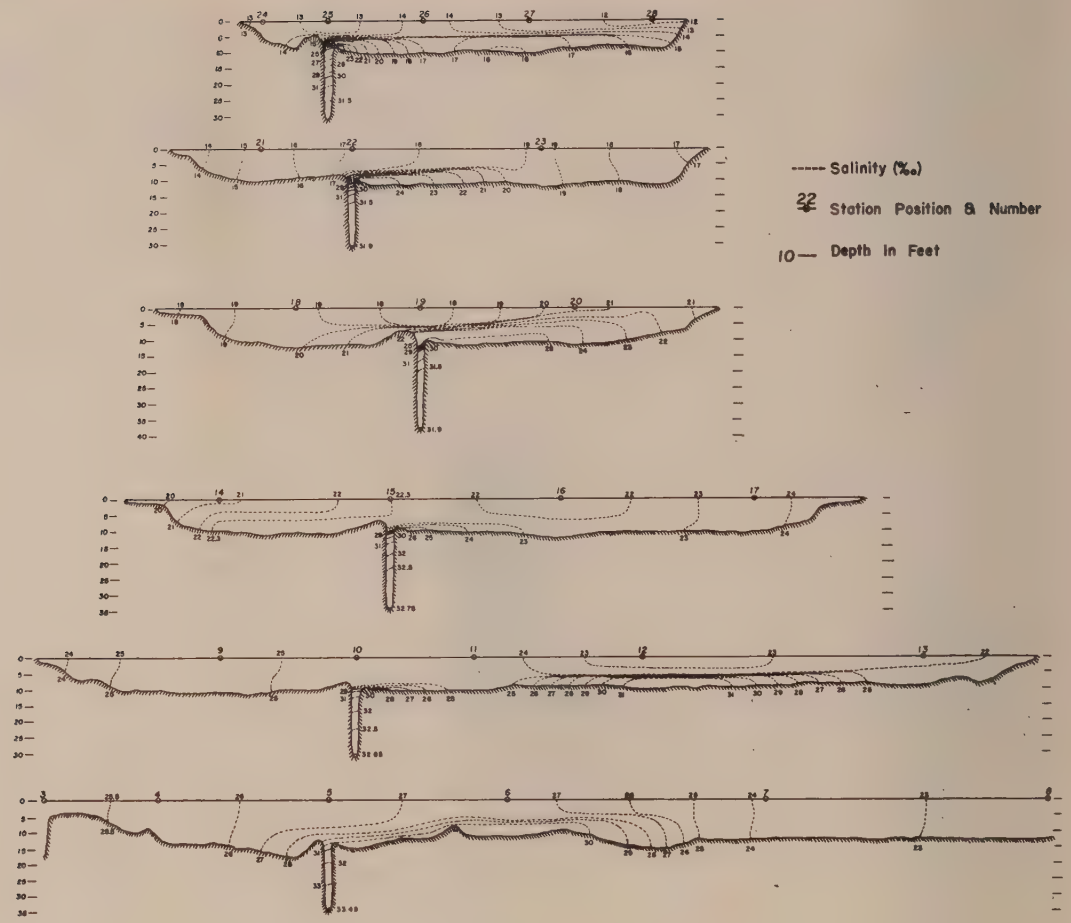


FIGURE 2

FIG. 2. Salinity-Depth Sections in Mobile Bay. The upper profile is a cross-section at Daphne, the next at Seacliff and the third south of Point Clear, all of which are in the area where jubilees occur. As the spoil bank of the ship channel is on the west of the channel, stratification is more marked on the east. (Figure reproduced from Austin, 1954, as was Figure 1).

with 0.24 ml/l occurring at 12 feet. The salinity gradually increased from 3.9 o/oo at the surface to 13.6 o/oo at the bottom. $CO_2$ also increased gradually from top to bottom.

Additional samples could not be obtained because weather became too rough for small boat operations or sampling.

## BIOLOGICAL OBSERVATIONS

Many people report seeing flounder and crabs swimming near the surface immediately preceding

TABLE IV.. Observations following a jubilee at Daphne July 12, 1957—Jubilee Occurred July 12—AM.

| Location | Time | Depth Ft. | Temp. °C | Sal. 0/00 | $O_2$ ml/l | $CO_2$ ml/l |
|---|---|---|---|---|---|---|
| 2 Mi. West of | 1330 | 0 | 31 | 3.9 | 6.44 | 0 |
| Daphne Warf | 1445 | 3 | — | 4.5 | 6.51 | 1.53 |
| " | 1400 | 6 | 30 | 6.9 | 4.97 | 0.86 |
| " | 1415 | 9 | 30 | 10.8 | 0.38 | 1.39 |
| " | 1430 | 12 | 30 | 11.9 | 0.29 | 2.24 |
| " | 1250 | 12 | — | 13.6 | 0.24 | 2.55 |
| " | 1345 | 12 | — | — | — | 2.55 |

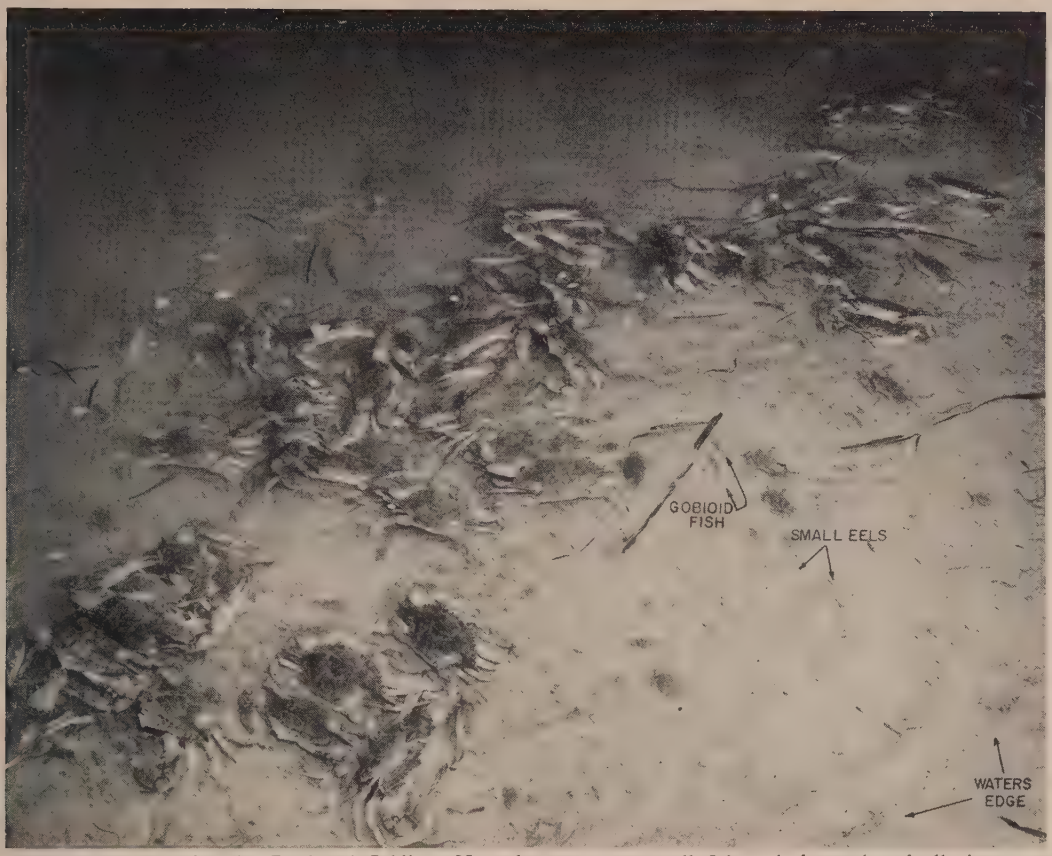


FIG. 3. At Water's Edge During A Jubilee. Note the numerous small fish and the crabs of all sizes.

a jubilee. During the time of the sampling reported in Table IV, many small crabs and fish were observed swimming at the surface and in an area of about 16 ft X 16 ft; an average of 4 small crabs were visible at one time.

Mortalities are rare and the people are not reluctant to eat fish and crabs taken during a jubilee.

Species typically affected are demersal. Worm eels, crab, shrimp, stingaree, and flounder are the types most often reported.

Some interesting observations were made on marine animals in the presence of water known to be oxygen deficient during a rotenone poisoning of Deer River, a tidal stream on the west shore of Mobile Bay. Flounder were observed to slither up the banks, and the blue crabs were observed actually climbing tree stumps to escape the water. This reaction is very similar to that which occurs during a jubilee.

## HYPOTHESIS

From Figure 1, which shows a current pattern in Mobile Bay, the convergence of river water and lower bay water can be noted in the area in which jubilees most often occur. A gentle east wind during the day preceding a jubilee would not produce sufficient wave action to mix the water near shore, especially since bluffs of a height up to 100 feet bound the shoreline in this area. However, the wind would be sufficient to push the surface water west and offshore. As this water moves off, it is replaced by the more saline deeper water.

Figure 2, reproduced from Austin (1954), shows a pocket of high salinity water in the deep water in this region. As the top fresher water is gently pushed offshore, it is this pocket of saltier water that replaces it.

A regular sampling station was located a few hundred feet from shore in this area. This station was sampled monthly by shrimp trawl from July 1953 to September 1955. The 30-minute trawl at this station often resulted, especially in summer, in a tub or more of small pieces of wood and debris an inch or two long. Also, this station would yield very few fish or shrimp, and occasionally none, in summer. The summer rot-

ting of the accumulation of debris here would result in low oxygen content in this water. During the day plant forms in the water would produce $O_2$ and use $CO_2$. When this process reversed at night a further decrease in $O_2$ would result.

As this body of stagnant deeper water moves toward shore, aided by a rising tide, to replace the surface water being pushed offshore by an east wind, the demersal animals move in advance of this body of water. When, under these conditions of east wind and rising tide, this body of deeper water moves very close to shore the demersal animals crowd to the shore, becoming more concentrated, and a jubilee is in progress.

## Summary

The Mobile Bay jubilee, in which crabs, shrimp, some fish, and other estuarine types (Figure 3) crowd to the edge of the water at infrequent intervals during summer months chiefly along the northeast shore, occurs most frequently during the dark hours on a rising tide following a day of east wind. The coincidence of these climatological conditions results in an inshore movement of water which is low in $O_2$ because of the rotting of wood debris accumulated from the Tensaw River runoff from a deep pocket near the eastern shore of the bay. Demersal animals especially move inshore ahead of this water mass. Changes in tide, wind, or other meteorological conditions result in water aeration and terminate the jubilee. Mortalities are rare.

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# GROWTH AND DEVELOPMENT IN PHALARIS. I. VERNALIZATION RESPONSE IN GEOGRAPHIC STRAINS OF *P. TUBEROSA* L.

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## Introduction

The introduced *Phalaris tuberosa* has proved successful as a pasture grass in Southern and Western Australia and in the areas with effective winter rainfall of Eastern Australia. Its natural distribution is restricted to the Mediterranean area (Hartley and Williams 1956). In Australia a plant introduction and breeding program has been started with the aim of obtaining strains superior to that presently used, which is referred to in this paper as Australian Commercial. For such a program it is necessary to have available a wide range of strains. These have been assembled as the result of two seed-collecting trips to the Mediterranean countries. When the introductions were grown in the same environment, they appeared to differ from each other in many ways, for example, in morphological characters, in distribution of growth over the year, in length of growing period, and in flowering time.

In this paper "flowering" is defined as the presence of an emerged inflorescence. Low temperature induces a plant. The induced plant or meristem then requires suitable photoperiodic or temperature conditions for development of an inflorescence and for emergence of that inflorescence (realization phase). Flowering time can, therefore, be determined by a number of factors affecting either the inductive process or the realization

[1] Part of the work was carried out when the author was an officer of the Division of Plant Industry, C.S.I.R.O., Canberra, Australia.

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phase or both. The present paper reports efforts to determine if the amount of cold required for induction is important in regulating flowering time under natural conditions. The results appear to show that this cold requirement of a Phalaris population is closely related to the climatic conditions of the place of origin. In addition to its ecological significance, the information obtained can be usefully employed in a breeding program. Also, as Cooper (1950) has pointed out, time and extent of heading are important characteristics of herbage grasses from a practical point of view.

## Material and Methods

The geographical strains were obtained by J. F. Miles and C. M. Donald (Div. of Plant Industry, C.S.I.R.O., Australia) during a collecting expedition in 1951. From a limited number of their collections, seed has been produced under isolation, and this seed has been used in the experiments. Table I gives particulars on the origins of the strains. In addition to these introductions, an Australian Commercial strain (V94) has been included in most of the experiments.

Table I. Details of the origin of the strains.

| CPI No. | Country | Place | Altitude m | Mean annual temp. °C | Mean temp. of the coldest month | Emergence in the field[1] |
|---|---|---|---|---|---|---|
| 14057 | Israel | Jerusalem | 820 | 17.5 | 8.9 | 301 |
| 14072 | Italy | Bovino | 100 | 16.0 | 5.0 | 317 |
| 14279 | Greece | Plain of Xineon, North of Lamia | 400 | 14.4 | 3.4 | 325 |
| 14418 | Portugal | Arronches | 300 | 15.9 | 8.4 | 313 |
| 14419 | Portugal | Tomar | 150 | 15.0 | 8.6 | 320 |
| 14495 | Algeria | Mangin | 108 | 17.7 | 10.6 | 301 |
| 14498 | Algeria | Tadmit | 1100 | 13.3 | 4.3 | 302 |
| 14693 | Morocco | Souk el Arba du Rharb | 50 | 17.4 | 10.9 | 315 |
| 14696 | Morocco | Tarmilet | 1200 | 15.0 | 7.5 | 315 |
| 15021 | Turkey | Izmir (Smyrna) | 80 | 17.3 | 8.2 | 318 |
| 15022 | Turkey | Istanbul | 0 | 13.7 | 4.5 | 323 |
| 15311 | Israel | Mt. Ephraim | 290 | 18.6 | 11.2 | 301 |

[1] Emergence of the inflorescence in the field at Canberra, Australia (expressed as day of the year).

Cold treatment was given to seeds germinating on filter paper over saturated vermiculite or to seedlings growing in vermiculite and in the three-leaf stage at the beginning of the treatment. The vernalization temperatures were 2.5 or 4°C as indicated in the various experiments. In addition to these controlled treatments some introductions were sown outside in cold frames which were kept closed and warm until the plants reached the three-leaf stage. They were then exposed to the lower outside temperatures for different lengths of time.

Vernalization in light was carried out in artificial light. The light source consisted of fluorescent tubes (Slimline, warm white) interspersed with incandescent light bulbs. The light panel contained one 60W incandescent bulb for every two fluorescent tubes. The light intensity used was 800 ft. c.

After completion of the vernalization treatment the plants in all experiments were planted out in a greenhouse with a minimum temperature of 17 to 19°C and under a photoperiod of 16 hours, and were arranged according to a randomized block design. Control plants were placed in the testing greenhouse at the same age and morphological stage as those at which vernalization was commenced on treated plants. Through use of staggered sowings, control and treated plants could be transferred to the testing conditions simultaneously.

The effect of cold treatment was judged by noting the number of days from planting in the greenhouse to anthesis (appearance of anthers and stigmas on the emerged inflorescence) and by observing elongation of the tillers or production of inflorescences.

## Results

Treatment of germinating seeds in darkness at 2.5 or 4°C in a refrigerator appeared to have no effect on reproductive development but did retard vegetative growth. Table II summarizes the results obtained with such non-effective seedling vernalization. The percentage of plants which flowered irrespective of the duration of the cold treatment are given for each of 11 strains. Such lumping is possible because the differences among treatments were not significant. The total number of plants for each strain should be 75, but some plants died and others appeared to be different species of *Phalaris*.

Table II. Number of plants flowering after 240 days without effective cold treatment.

| CPI No. | Number of plants | % plants flowering |
|---|---|---|
| 14057 | 73 | 69.9 |
| 14072 | 74 | 4.2 |
| 14279 | 67 | 1.5 |
| 14418 | 74 | 45.9 |
| 14419 | 73 | 67.1 |
| 14495 | 75 | 90.7 |
| 14498 | 73 | 5.5 |
| 14693 | 71 | 42.3 |
| 14696 | 74 | 52.7 |
| 15021 | 69 | 76.8 |
| V94 | 71 | 11.3 |

The experiment of Table II shows that there are large differences between populations from

different geographic origins and that some populations apparently are quite heterogeneous. The proportion of plants which flower without effective cold treatment indicates the extent to which the population possesses no cold requirement. The rating of populations on this basis may differ from one based on the effect of various lengths of duration of the cold period. It is therefore necessary to obtain quantitative information about the length of the cold period required by the cold-requiring strains.

In preliminary experiments it had been found that seedlings in the three-leaf stage can be successfully vernalized in artificial light at 2.5 or 4°C. Quantitative data on response to cold have therefore been obtained by treating seedlings in the three-leaf stage. The experiments have been carried out in controlled environments. Seedlings of populations were grown to the three-leaf stage in a greenhouse at 26°C day temperature (for 8 hours) and 20° night temperature (for 16 hours) and a photoperiod of 16 hours. They were then kept for 0, 2, 4, 6, or 8 weeks at 4°C in artificial light, daylength 16 hours. After completion of the cold treatment the plants were transferred to a greenhouse at 23°C day temperature (for 8 hours), 17°C night temperature, and 16 hours daylength. The results of this experiment are summarized in Table III.

TABLE III. The effect of 0, 2, 4, 6, and 8 weeks of cold treatment (4°C) on the number of plants flowering after 120 days; 8 plants per treatment. Treatment given to seedlings in the three-leaf stage.

| CPI No. | Number of Plants Flowering | | | | |
|---|---|---|---|---|---|
| | 0 weeks | 2 weeks | 4 weeks | 6 weeks | 8 weeks |
| 14057 | 3 | 6 | 8 | 8 | 8 |
| 14072 | 1 | 3 | 5 | 6 | 8 |
| 14279 | 0 | 0 | 0 | 2 | 4 |
| 14418 | 3 | 4 | 6 | 8 | 8 |
| 14419 | 2 | 3 | 5 | 8 | 8 |
| 14495 | 6 | 8 | 8 | 8 | 8 |
| 14498 | 0 | 0 | 1 | 5 | 8 |
| 14693 | 0 | 0 | 0 | 6 | 8 |
| 14696 | 5 | 8 | 8 | 8 | 8 |
| 15021 | 4 | 5 | 7 | 8 | 7 |
| 15022 | 0 | 0 | 1 | 4 | 7 |
| 15311 | 4 | 7 | 8 | 8 | 8 |

It is evident that the strains differ in the amount of cold required for induction. This ranges from very low or no cold requirement (14495) to 8 weeks or more (14279) under the conditions of the experiment. The populations are not uniform with regard to cold requirement. The cold requirement of some individuals is more quickly satisfied than that of others. The cold requirement is absolute in the populations requiring a period of 8 weeks or longer at 4°C. The controls were maintained up to 2½ years under conditions conducive to flowering. At that time they were still vegetative. The majority of the non-vernalized plants of populations requiring 2 to 6 weeks of cold treatment will eventually flower, but it may take 8 to 12 months or longer. The relation between length of cold treatment required and the climate of the place of origin will be discussed later.

In order to get an idea of how the cold requirements found in the greenhouse compare with those in the field, a small experiment was carried out using "natural" vernalization. Seedlings were transferred from outside into the greenhouse at different times during the winter. Details of the growing conditions will be found on page 299. In this experiment strains 14495, 14498, 14279 and Australian Commercial V94 were used. Coastal Algerian types are represented by 14495 and collections from higher altitudes in Algeria by 14498. Strain 14279 originates in a more temperate area, while Australian Commercial was added as a standard. Details of the transfers can be found in Table IV, and the results are given in Tables V and VI. Transfer 1 is the control series.

TABLE IV. Details of the "natural" vernalization treatment.

| No. | Date of transfer | Natural daylength hours. min. | Total no. hours below 10° C |
|---|---|---|---|
| 1 | June 12, 1956[1] | 10.45 | 0 |
| 2 | July 24, 1956 | 11.09 | 938 |
| 3 | Aug. 27, 1956 | 12.06 | 1659 |
| 4 | Oct. 15, 1956 | 13.50 | 2449 |

[1] Date at which exposure to natural cold was started.

It is clear from Table V that the number of plants which elongate increases with length of previous exposure to winter temperatures. At the third transfer all plants of all strains elongated. Table V also shows that only some of the elongating plants produce inflorescences and that the proportion of non-flowering plants is considerably greater for transfers made in spring. This phenomenon has been observed in all transfer experiments of this type. In the greenhouse the number of "blinds" (elongating tillers which do not produce an inflorescence) is generally higher than in the field although certain introductions do produce a large number of blinds in the field. Two types of blinds can be clearly distinguished. Blinds of the first type produce a definite number of leaves which is equal to the number of leaves which would have been formed if the tiller had

developed an inflorescence. Often a rudimentary inflorescence can be found in the leaf sheath. This type of blind is most common. The second type produces leaves more or less indefinitely, and the leaves tend to become smaller. There is no sign of an inflorescence. This suggests that the former type of blind is due to something which upsets the development of the inflorescence, perhaps too high a temperature or a sudden change in temperature, while the latter may point to incomplete induction.

TABLE V. The effect of "natural" cold treatment on flowering; 15 plants per treatment. Scored November 30, 1956.

| | Number of Plants | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Elongating | | | | Flowering | | | |
| Transfer | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| 14495 | 8 | 15 | 15 | 14 | 8 | 15 | 14 | 2 |
| 14498 | 1 | 13 | 15 | 15 | 0 | 10 | 7 | 0 |
| V94 | 1 | 7 | 15 | 15 | 0 | 5 | 9 | 9 |
| 14279 | 0 | 1 | 15 | 14[1] | 0 | 0 | 10 | 0 |

[1] One plant died.

Table VI shows the days in the greenhouse required after transfer (from outdoor-winter temperature) to anthesis of the first head. The number of days required is inversely related to the length of cold treatment outdoors which (at least for transfers 2 and 3) indicates greater induction with more complete vernalization. The lesser number of days to anthesis between the third and fourth transfer could be wholly or partly due to the higher temperatures and lengthening days of spring and might have nothing to do with vernalization. The higher temperatures and longer days of spring could cause the start of development of the inflorescence and elongation of the internodes. The plants would thus be in an advanced stage of development when they were transferred into the greenhouse.

It appears that 14495 does not have a very high requirement for cold since in the control 8 out of 15 plants flowered. But its flowering is accelerated by vernalization under natural conditions. Nos. 14498 and V94 have a similar cold requirement, that of 14498 probably being more easily satisfied since it produced more flowering plants after the second transfer. No. 14279 obviously has a very high cold requirement. It would appear that induction of these populations is fairly complete by the time of the third transfer. Also, the results from the natural vernalization experiment are in good agreement with the results of the quantitative experiment shown in Table III.

TABLE VI. Number of days required, following natural vernalization, after transfer to long day and high temperature until anthesis. (Average for the number of plants flowering shown in Table V).

| Transfer No. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| 14495 | 103.3 | 58.6 | 48.1 | 39.0 |
| 14498 | — | 74.2 | 48.0 | —[1] |
| V94 | — | 88.5 | 53.7 | 40.4 |
| 14279 | — | — | 65.6 | —[1] |

[1] None of the plants produced an inflorescence.

One might ask what role the short days of winter play in the floral induction of Phalaris by exposure to natural winter conditions. It appears from the experiments described that short days are not required for induction because the plants can be fully induced by cold treatment under long-day conditions. However, short-day treatment by itself can replace vernalization to some extent, but it generally takes a much longer time for induction to take place and the subsequent development of the plants is much slower than after vernalization. For example, in Australian Commercial V94, two months of short days (8 hours light) under conditions of day temperature 23°C and night temperature 14°C gave an induction of 30% of the plants, compared to no induction of plants kept under the same temperature conditions but under long days (16 hours light). Comparable results were obtained with 17°C night temperature. Two months cold treatment would have resulted in complete induction of all plants. Again, the flowering plants were detected by dissection 6 weeks after transfer to long-day condition in cold requirement of *Phalaris* strains even had emerged inflorescences. Apparently the role of short days is not very significant under normal conditions when a sufficient amount of cold is available.

## Discussion

The experiments described show a wide variations. At this time vernalized plants would have though the species has a limited geographic distribution. Even for strains originating in relatively close proximity there are large differences in cold requirement, for example, the Algerian introductions 14495 and 14498. On the basis of the present experiments the introductions may be ranked according to their cold requirement.

It may also be noted that the non-vernalized series of Tables II and III yield different results. This is caused in part by the differences in length of time of observation. The results given in Table II are based on a final observation after 240 days of growth under conditions conducive to flower-

ing. Table III has been based on a final observation after 120 days. However, even when comparisons are made at equal days after transfer to long-day, high-temperature conditions, the differences in behavior between Table II and Table III persist. This may well be caused by differences in seed source. The experiment of Table II was done with seed of a different year from that used for the experiment of Table III. Since vernalization of the ripening seed on the parent plant is possible (Gregory and Purvis 1938), time of harvesting and time of seed maturation may be related to these variations. Another cause of the difference is the level of temperature during growth. By bringing together the results from experiments done for various purposes under controlled environments, as has been done in Table VII, it can be seen that the number of plants which flower without cold treatment is determined by the temperature conditions prevailing during the period of development. In general, the higher the temperature, the lower the proportion of plants which flower, except possibly for the strains which have a very low cold requirement. Strains with a very high cold requirement, for example, 15022, 14498 and 14279, are not much affected either. The effect of temperature may be due to "devernalization" (loss of the partly vernalized condition of the seed which originated as described above) during growth under high temperatures. The phenomenon could be important in the comparison of experiments done at different times of the year or in different years. It might be possible to overcome the difficulty by exposing the seedlings, both controls and treated, to a constant temperature of, for example, 15°C for some days before they are planted out in the greenhouse (Purvis and Gregory 1952). An alternative explanation could be provided by the interaction between photoperiod and temperature as found by Aitken (1955). She reported that in some varieties of *Trifolium subterraneum* L. a long photoperiod can replace cold treatment, or, stated in another way, that long photoperiods raise the level of temperature which may act as a low temperature in causing floral induction. Applied to the present results, one could say that some strains require a longer daylength to flower at the higher temperatures, or else, that at a daylength of 16 hours the high temperatures are too high to effect induction.

It is of interest to ascertain which climatic factors are related to the cold requirement of the populations of different geographical origin. Some climatic characteristics of the places of origin have been given in Table I. It appears that when we consider the present range of strains from the entire Mediterranean area, there is no correlation of cold requirement with altitude. This may be different for introductions collected from smaller areas. Unpublished experiments on a large number of Algerian introductions from a relatively small area show that the cold requirement increases with increasing altitude. However, this can be explained in terms of the correlations found for the present experiments, because the temperature decreases with increasing altitude. There is a good correlation between cold requirement and average annual temperature or, even better, average temperature of the coldest month. The latter relationship is shown in Fig. 1. The correlation factor between vernalization requirement and average temperature of the coldest month for the experiment shown in Table IV is — 0.95. The lower the average temperature of the coldest month, the higher the amount of cold required for complete induction of the whole population. There seems to be no point in trying to bring in factors other than temperature, for example rainfall or length of growing season, since they cannot contribute much more to the correlation between climate and cold requirement. Moreover, in most cases the meteorological information available is not sufficiently accurate or detailed to permit assessment.

Some introductions need more comment. CPI 14693 has not been used in the calculations of the correlation factor since this introduction is probably not indigenous to the area in which it was collected. It differs in many respects from the other Moroccan material and, although it was collected in a coastal location with fairly high average

TABLE VII. The effect of temperature on the number of plants which flower without cold treatment. The first temperature given in each column is the day temperature (for 8 hours every day) the second one is the night temperature. Each value is based on 18 plants. Scored after 80 days.

| CPI No. | Temperature °C | | |
|---|---|---|---|
| | 20/14 | 26/20 | 30/23 |
| 14057 | 11 | 7 | 7 |
| 14072 | 2 | 0 | 0 |
| 14279 | 0 | 0 | 0 |
| 14418 | 9 | 8 | 5[1] |
| 14419 | 16[1] | 13 | 10[2] |
| 14495 | 13[1] | 16 | 13[1] |
| 14498 | 1 | — | 0 |
| 14696 | 11[1] | 6 | 6 |
| 15021 | 8 | 11 | 9 |
| 15022 | 1 | — | 0 |
| 15311 | 12 | 11 | 8 |

[1] Based on 17 plants.
[2] Based on 16 plants.

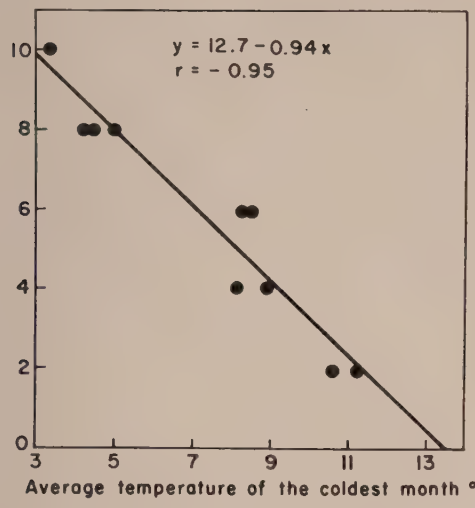


FIG. 1. The relation between cold requirement and the mean temperature of the coldest month. The regression equation is given in the figure. It is considered that the whole population has been induced when 7 out of 8 plants flower.

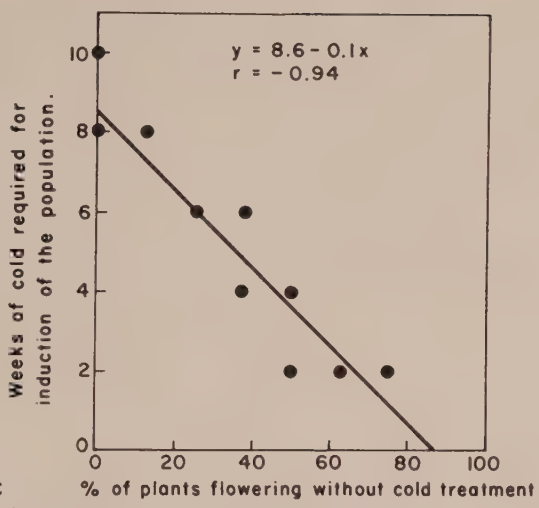


FIG. 2. The relation between the proportion of plants which flower without cold treatment and the cold treatment required for complete induction.

temperature, it possesses the highest cold requirement found among the Moroccan material. In addition, it was collected in an area in which sown plots of grass species were maintained on a farm. It may well therefore represent an escape rather than an indigenous form. Another exception is 14696 for which the cold requirement which satisfies the whole population is low as compared to the average temperature of the coldest month of its place of collection. This will be investigated further since more extensive testing of a wide range of Moroccan material is in progress and 14696 has been incorporated in this series.

Another point which needs clearing up is the extent to which the number of plants which flower in a control series which has had no cold treatment is indicative of the cold requirement of the population. The fact that a very small proportion of plants flower in a non-cold-treated series of plants does not necessarily mean that the population as a whole requires a large amount of cold to reach competence to flower. It may only indicate that the population is rather homogeneous for cold requirement but that the population as a whole is completely induced by a relatively short period of vernalization. Figure 2 shows the relation between the number of plants which flower in a control series without cold treatment and the number of weeks of cold treatment required to induce flowering of the population. The correlation is quite good. A correlation factor of — 0.94 has been found for the relation between weeks of vernalization required and the percentage of plants flowering without cold treatment in the case of the data shown in Table IV. The high correlation would justify the testing of a large number of ecotypes for cold requirement by merely noting the fraction of plants which flower without cold treatment. If one is interested in populations with high cold requirement, strains of which a low proportion of the plants flower without cold treatment can be selected and then further tested in a quantitative manner. The correlation between the number of flowering plants and the average temperature of the coldest month is also high. This appears from the regression lines given in Figures 1 and 2.

A question which remains is the extent to which cold requirement functions as a regulating factor for flowering time. It is difficult to answer this question for the places of origin because sufficient data about flowering time and climate are not available. However, one can compare the data of Table III concerning cold requirement and the data on flowering time of the same strains under field conditions at Canberra, Australia (Table I, last column). It is obvious from such a comparison that high cold requirement does not necessarily correspond with late flowering or the reverse. For example, 15021 and 15022 are equally late in flowering. However, 15021 has a low cold requirement while 15022 has a high cold requirement. The same holds true for 14495 and 14498. It is true though that low vernalization requirement is more common among the early flowering strains than it is among the late flower-

ing ones. It appears that when the strains are grown together in the same environment they differ in flowering time, even though they have the same cold requirement. Under natural conditions in this particular environment, a plant will flower in October or November, therefore in spring. Even when cold treatment is not started until the middle of June, when winter is well on its way, all the populations have been fully vernalized by September (Table V and VI). In other experiments (unpublished data) cold treatment was started outside in April, when temperatures below 10°C first occur. It appeared that all strains, even those of highest cold requirement, were fully cold-treated by the middle of June. This can be interpreted as an indication that under Canberra conditions vernalization does not play a part in the determination of flowering time. Flowering time must be determined by daylength or spring temperatures, or both. At Canberra presumably spring temperatures rather than daylength determine flowering time. In warmer climates daylength may be the limiting factor. The importance of spring temperature is emphasized by the fact that *Phalaris tuberosa* flowers earlier when grown in areas with an earlier, warmer spring. It may be justified to assume that under natural conditions in the places of origin the flowering time is not determined by vernalization either, but as yet there is not sufficient evidence to state this as a fact. When the strains are transferred to a warmer environment, particularly those strains which have a high cold requirement, it may well happen that they do not receive sufficient cold for flowering to occur. In those cases vernalization requirement will limit or determine flowering time.

Although there is as yet little evidence indicating that cold requirement is important in the determination of flowering time, it is possible that the interaction of cold requirement with spring temperatures and daylength will determine flowering time, and not any one of these factors independently. This seems to be unlikely in the Canberra environment, because cold requirement is satisfied early in the season. In the natural environment such a system could operate very effectively. This hypothesis has yet to be tested experimentally. Genetic differences in rate of development of the inflorescence and in sensitivity of rate of development to temperature may also play an important role.

It can be concluded from these experiments that within *Phalaris tuberosa* differentiation of strains exists, comparable to that, for example, found in *Lolium* (Cooper 1951). The differentiation occurs in morphological characters as well as in physiological properties. In the case of cold requirement for flowering the correlation with environment is quite close. Vernalization can be called the inductive process and the subsequent initiation and development of the inflorescence, triggered off by suitable photoperiod and affected by temperature, the realization phase. One can imagine that either of these phases or both together will determine flowering time. However, it appears that in the case of *Phalaris tuberosa* induction is normally complete and does not limit further development. Apparently flowering time is determined by factors affecting the realization phase, or by interaction of a number of environmental factors affecting either the inductive process or the realization phase or both.

## Summary

The physiology of flowering of geographic strains of *Phalaris tuberosa* L. collected from all over its native range has been studied with particular reference to the amount of cold required for induction of flowering. The strains differ widely in this respect. Some strains have practically no cold requirement, while the cold requirement of others can be satisfied only by maintaining the seedlings at 4°C for 8 weeks or longer. All intermediates occur. A check experiment, using natural vernalization, gave essentially the same results as experimental vernalization in cold rooms under artificial light. No correlation has been found between cold requirement and altitude of the places of origin in the present material. The correlation between cold requirement for complete induction and mean temperature of the coldest month is high (— 0.95). The importance of cold requirement for the regulation of flowering time has been discussed, and it has been concluded that this depends on the conditions under which the plants are grown, but that under field conditions in Canberra (Australia) vernalization does not limit the flowering process. Here photoperiod and spring temperatures will be the determining factors, probably with emphasis on temperature. The alternative hypothesis that flowering time will be determined by the interaction between cold requirement, spring temperatures and photoperiod has yet to be tested. Such a system might be of great importance for strains growing in their native environment. Many of the populations are not genetically uniform with regard to cold requirement. The correlation between the proportion of plants which flower without cold treatment and the amount of cold required to induce flowering in

the whole population is high. This may be used to obtain a rapid indication of the approximate amount of cold required.

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# DIFFERENTIAL RESPONSES OF THREE SPECIES OF THE ANNUAL GRASSLAND TYPE TO PLANT COMPETITION AND MINERAL NUTRITION.[1]

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Changes in botanical composition of grassland communities in response to nutrient application are common and widespread. They generally result from differential responses of species to the added nutrients and from reciprocal interactions of associated plants. The latter is encompassed within the concept of plant competition in this paper.

Numerous workers have reported on the relative effects of plant competition and nutrients in mixed grassland stands. Most reports have been concerned with mixtures of leguminous plants and grasses in field plots. Blackman (1938) studied the effects of competition in mixed stands of *Trifolium repens* and grass species by varying light intensity and rates of applied nitrogen. He concluded that competition of grasses reduced clover when additional nitrogen was applied but the mechanism of this competition was obscure. Blaser and Brady (1950) applied nitrogen and potassium to mixed stands of several grasses and legumes. Leguminous plants were reduced when nitrogen was applied. The authors concluded that reduction resulted from competition with grasses for potassium. In this instance potassium became limiting before any other factor in relations among the grasses and legumes.

Donald (1951) studied the effect of intraspecific competition on yields of *Trifolium subterranean* and *Lolium rigidum*. His experiments consisted of field trials in which the 2 species were planted separately and at different densities. Results indicated that intraspecific competition among these plants increased with density, with advancing stage of growth, and with decreased nutrients.

In this study, the interrelation of responses of 3 nonleguminous species of an annual grassland community, *Bromus mollis, Erodium botrys,* and *Festuca megalura,* were investigated relative to nitrogen and phosphorus treatments and plant competition. These species were selected because each responds differently to nitrogen application in the field and each has different growth characteristics. *B. mollis* is a comparatively large, wide-leaved grass; *F. megalura* is a small, narrow-leaved grass; and *E. botrys* is a broad-leaf plant with a semiprostrate growth habit. Field studies have shown that *B. mollis* and *E. botrys* generally increase in percentage of the stand with added nitrogen while *F. megalura* decreases. When these dissimilar species are studied, differences in shading and differential nutrient uptake constitute factors of plant competition. Both intra- and interspecific competition were studied. To define more precisely the species relations the following adjectives are used: monospecific, with plants of one species in association; bispecific, with plants of 2 species in association; and trispecific, with plants of 3 species associated.

## Procedure

Plants were grown in 6 in. pots in a greenhouse. Ceramic pots and saucers were coated inside and

[1] The material reported in this paper is taken from the author's dissertation for the Ph.D. degree from the Department of Botany, University of California, Berkeley. The encouragement and guidance of Professors H. L. Mason, R. M. Love, and A. S. Crafts are gratefully acknowledged.

out with black asphalt varnish. Pots were also painted on the outside with aluminum enamel. The general procedure followed that of Jenny *et al.* (1950).

The soil was representative of the Laughlin series: a slightly acid prairie soil of clay loam texture varying in depth from 2 to 3 ft. Soil samples were taken to a depth of 8 in. The soil was thoroughly mixed and sieved through ¼ in. mesh screen. Seed was collected from plants growing on Laughlin soil.

The 3 species were grown monospecifically, bispecifically, and trispecifically with combinations of 6, 12, and 24 plants per pot. In bi- and trispecific combinations equal numbers of plants of each species were grown.

Factorial combinations of 5 rates of nitrogen and 2 of phosphorus, including the control, were used. Nitrogen was added at 4, 8, 16, and 32 mg per pot (50, 100, 200, and 400 equivalent lbs. per acre). Phosphorus was applied at 16 mg $P_2O_5$ per pot (200 equivalent lbs. per acre). Added nutrients in the pots were converted to equivalent field amounts on the basis of soil weight to the depth of 6 in. (Jenny *et al.* 1950). Ammonium nitrate ($NH_4NO_3$) was used as the nitrogen source and monocalcium phosphate ($CaH_2PO_4 \cdot H_2O$) as the phosphorus source. Water solutions of these salts were added to the soil surface.

Plants were grown 16 weeks during summer and early fall. Aerial portions were harvested, oven-dried and weighed. Yields were expressed in terms of oven-dry weight of plant material of individual species per pot. Variables of the pot test were arranged in a randomized-block factorial design (Cochran and Cox 1950). Species-combination and nutrient-treatment effects were analyzed by analysis of variance. The effects of different numbers of plants per pot were analyzed by Bartlett's test of homogeneity of variances (Bartlett 1937).

Chemical analyses were made on samples of the plant material to determine total nitrogen, nitrate nitrogen, and phosphate or soluble phosphorus. Total nitrogen was determined by the Kjeldahl method (Assoc. Official Agr. Chem., 1955). Methods of Johnson and Ulrich (1950) were followed in determining nitrate nitrogen. Phosphate phosphorus was determined by the acetic acid method of Fiske and Subbarrow (1925).

Random portions of the soil sample were composited for physical and chemical analyses. Percentages of gravel, sand, silt, and clay were determined by the method of Bouyoucos (1928). Total-nitrogen percentages were determined by techniques in Methods and Analysis, Association Official Agricultural Chemists Ed. 6 (1945). The Bingham (1949) test was used for percentage of water-soluble phosphorus.

## Results and Discussion

### *Yields of Species*

Applied nitrogen increased yields of the 3 species in a similar manner and at a like magnitude when they were grown monospecifically. Bi- and trispecific competition among the species affected yields when nitrogen was applied at the 100, 200, and 400 lb. rates (Figs. 1, 2, and 3).

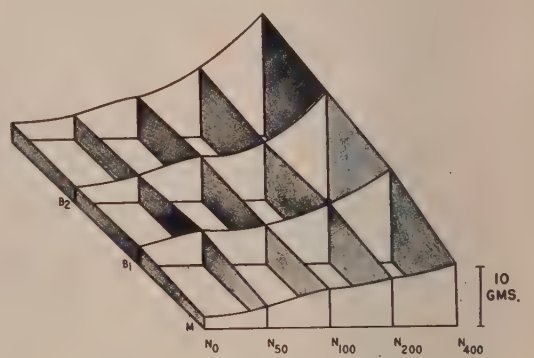


Fig. 1. Adjusted yields of *E. botrys* relative to interspecific competition and nitrogen treatment. M represents monospecific yield, $B_1$ bispecific yield with *B. mollis*, $B_2$ bispecific yield with *F. megalura*, and T trispecific yield. Rates of applied nitrogen range from 0 ($N_0$) to 400 pounds per acre ($N_{400}$). Yields in terms of oven-dry shoot growth adjusted to equal soil volume per species for each interspecific combination, i.e. monospecific yield of each species per pot x 1, bispecific yield of each species per pot x 2, and trispecific yield of each species per pot x 3.

Added phosphorus increased yields of all species. However, in terms of yield, phosphorus application did not alter relations between nitrogen levels and interspecific competition. Therefore, yields of species with and without added phosphorus are combined in the nitrogen-competition comparisons.

Monospecific yields of species are used as bases in all comparisons of yield differences resulting from interspecific competition. Comparisons are made in terms of adjusted yield per volume of soil, i.e., on a pot basis, bispecific yields are multiplied by 2 and trispecific yields by 3 to make them comparable to monospecific yields in terms of soil volume per species.

The following relations of interspecific competition, in terms of adjusted yields, were significant as shown by statistical analyses.

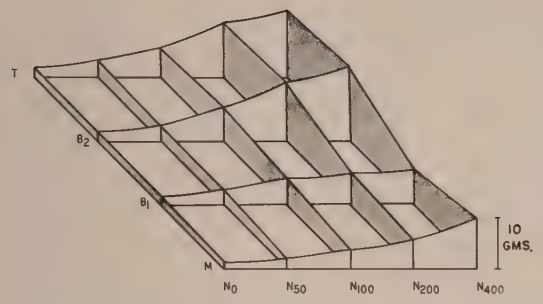


FIG. 2. Adjusted yields of *B. mollis* relative to interspecific competition and nitrogen treatment. M represents monospecific yield, $B_1$ bispecific yield with *E. botrys*, $B_2$ bispecific yield with *F. megalura*, and T trispecific yield. Rates of applied nitrogen range from 0 ($N_0$) to 400 pounds per acre ($N_{400}$). Yields in terms of oven-dry shoot growth adjusted to equal soil volume per species for each interspecific combination, i.e. monospecific yield of each species per pot x 1, bispecific yield of each species per pot x 2, and trispecific yield of each species per pot x 3.

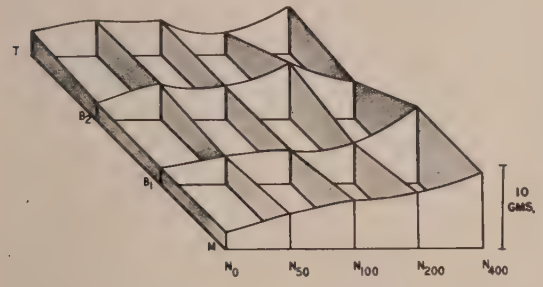


FIG. 3. Adjusted yields of *F. megalura* relative to interspecific competition and nitrogen treatment. M represents monospecific yield, $B_1$ bispecific yield with *B. mollis*, $B_2$ bispecific yield with *E. botrys*, and T trispecific yield. Rates of applied nitrogen range from 0 ($N_0$) to 400 pounds per acre ($N_{400}$). Yields in terms of oven-dry shoot growth adjusted to equal soil volume per species for each interspecific combination, i.e. monospecific yield of each species per pot x 1, bispecific yield of each species per pot x 2, and trispecific yield of each species per pot x 3.

Adjusted yield of *E. botrys* was not decreased at any level of nitrogen as a result of bi- or trispecific competition (Fig. 1). Increases in adjusted yield resulted from bispecific competition with *B. mollis* and *F. megalura* and from trispecific competition at the 400 lb. level of applied nitrogen. Also a slight increase resulted from trispecific competition at the 200 lb. level of added nitrogen.

Decreased adjusted yield of *B. mollis* resulted from bispecific competition with *E. botrys* at the 400 lb. level of applied nitrogen (Fig. 2). Adjusted yield increases were noted at the 100, 200, and 400 lb. levels of applied nitrogen as the result of bispecific competition with *F. megalura*. Trispecific competition increased the adjusted yields of *B. mollis* with 200 and 400 lb. of added nitrogen.

No increases in adjusted yield of *F. megalura* resulted from bi- or trispecific competition (Fig. 3). Decreases in adjusted yield resulted from bispecific competition with *B. mollis* at the 200 lb. level of applied nitrogen, bispecific competition with *E. botrys* at the 400 lb. level of applied nitrogen, and trispecific competition at the 100, 200, and 400 lb. levels of added nitrogen.

Adjusted yields of the 2 grasses growing with *E. botrys* in response to added nitrogen, were also affected by different densities. The variances of both *F. megalura* and *B. mollis* were significantly different in relation to density when these species were grown in bispecific competition with *E. botrys*. In no other relation did density affect adjusted yields of species.

From the preceding adjusted yield relations a definitive order of competitive ability of the 3 species under specific levels of applied nitrogen can be ascertained. Under the high nitrogen regime (400 lb.) this order places *E. botrys* highest, *B. mollis* intermediate, and *F. megalura* lowest. With 200 lb. of applied nitrogen *B. mollis* was most competitive with *F. megalura* and equal to *E. botrys* in bispecific relation with each of the species respectively. In bispecific relations, interspecific competition was not effective in altering yields below the 200 lb. level of applied nitrogen.

When the species were grown in trispecific relation *F. megalura* was the least competitive at the 100, 200, and 400 lb. levels of applied nitrogen. *B. mollis* was most competitive at the 200 lb. level. *B. mollis* and *E. botrys* were apparently equally competitive at the 100 and 400 lb. levels of applied nitrogen. Trispecific competition did not alter yields below the 100 lb. level of applied nitrogen.

Characteristics of *E. botrys* which might influence its competitive ability are rapid emergence and early growth, vigorous and large total growth, and large, wide leaves, which tend to shade associated plants. Importance of the shade factor, between this plant and the grasses, is emphasized by differences in response of the grasses to applied nitrogen which resulted from different densities. Figs. 4 and 5 illustrate the effects of *E. botrys* on the 2 grass species at different levels of added nitrogen.

*B. mollis* is characterized by rapid, large growth favorable for nitrogen extraction especially at higher levels. *F. megalura* also has the characteristic rapid growth of an annual and under ideal conditions, even with high levels of applied nitrogen, yielded the same as the other 2 species. However, under environmental stress resulting from in-

FIG. 4. Growth of *B. mollis*: upper, grown monospecifically; lower, grown bispecifically with *E. botrys*. Rates of applied nitrogen 0 ($N_0$) to 400 pounds per acre ($N_{400}$). Rate of applied phosphorus 200 pounds per acre $P_2O_5$ ($P_{200}$). Twenty-four plants grown per pot.

FIG. 5. Growth of *F. megalura*: upper, grown monospecifically; lower, grown bispecifically with *E. botrys*. Rates of applied nitrogen 0 ($N_0$) to 400 pounds per acre ($N_{400}$). Rate of applied phosphorus 200 pounds per acre $P_2O_5$ ($P_{200}$). Twenty-four plants grown per pot.

terspecific competition, yields of this species were reduced.

*Nitrogen and Phosphorus Percentages of Species*

Soil analyses indicated that the levels of nitrogen (0.09%) and phosphorus (0.128 ppm) were low in soil used in the experiment. Also, significant yield increases were obtained from added nitrogen and phosphorus in a pot test with several different grassland species as indicators. Neither added potassium nor sulfur gave yield increases. Further, from responses of plants to added nitrogen and phosphorus in this experiment, it was concluded that no micronutrient became limiting within the prescribed nutrient regimes.

At time of harvest, nitrate nitrogen content in all plants was below the experimental error of the method of analysis.

Percentages of total nitrogen in the 3 species under all types of competition increased similarly with greater applications of nitrogen when no phosphorus was applied. With added phosphorus, per cent total nitrogen did not increase relative to applied nitrogen. Standard deviation of total nitrogen percentages with no added phosphorus was 0.15 to 0.41 through all rates of applied nitrogen. With added phosphorus this standard deviation was more regular: 0.12-022% (Fig. 6). The 0.41% standard deviation, which is almost twice that of any other, occurred at the high level of nitrogen with no added phosphorus. This variation can be almost wholly accounted for by bi- and trispecific competition of the 2 grasses with *E. botrys*. Nitrogen percentage in *B. mollis* was reduced from 3.16 in monospecific competition to 1.98 in bispecific competition with *E. botrys*, and to 1.91 in trispecific competition. Nitrogen percentage was reduced from 2.18 to 1.64 and 1.55 in *F. megalura* under the same conditions. The nitrogen percentage in *E. botrys* did not vary in these instances. These relations correspond to the effects of bispecific competition between *E. botrys* and *B. molis* and *E. botrys* and *F. megalura* in terms of yield at the high rate of nitrogen with applied phosphorus. With no added phosphorus, similar yield relations occurred but at much lower magnitude. Most other differences in nitrogen percentage resulted from normal variation among species. These occurred especially at low levels of nitrogen.

Variation in phosphorus percentage in the 3 species with all types of competition was more or less regular in relation to nitrogen levels and was of less magnitude with no added phosphorus (Fig. 7). At the 200 lb. phosphorus level, without added nitrogen, where the standard deviation was largest (0.09%), there was a reduction in the phosphorus percentage in *F. megalura* from 0.46 in monospecific competition to 0.24 in trispecific competition. The phosphorus percentage in *B. mollis* was unchanged with competition. Phosphorus percentage increased in *E. botrys* from 0.47 in monospecific competition to 0.57 in trispecific competition. No other recognizable trend occurred in variation of phosphorus per cent attributable either to competition or to species differences. These changes in phosphorus percentage resulting from competition were slight compared with changes in percentage which resulted when phosphorus was added to the soil.

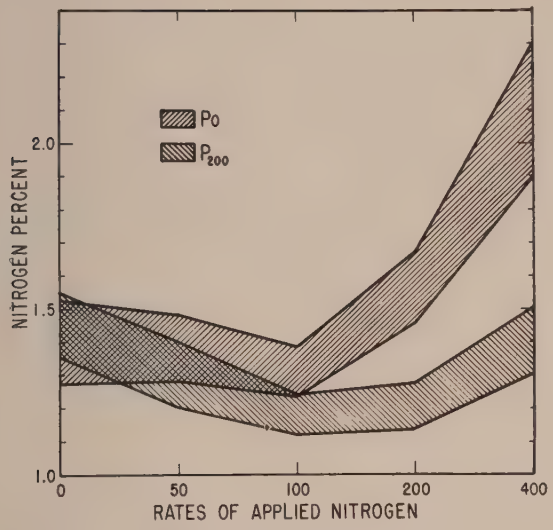


FIG. 6. Mean responses to nitrogen treatment of the 3 species, *B. mollis, E. botrys,* and *F. megalura,* at 2 levels of phosphorus, in terms of nitrogen percentage. Width of bands indicates standard deviation resulting from variation of different species and different types of competition in the experiment.

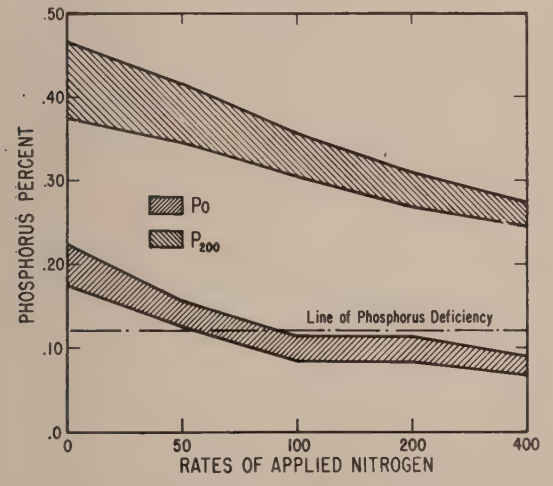


FIG. 7. Mean responses to nitrogen treatment of the 3 species, *B. mollis, E. botrys,* and *F. megalura,* at 2 levels of phosphorus, in terms of phosphorus percentage. Width of band indicates standard deviation resulting from variation of different species and different types of competition in the experiment.

At the 100 lb. level of applied nitrogen, without added phosphorus, phosphorus percentage in all 3 species decreased to about 0.10 (Fig. 7). From this point nitrogen percentage increased in direct relation to added nitrogen (Fig. 6). With added phosphorus, the minimum mean phosphorus percentage was 0.26. The yield when phosphorus was not applied increased little at levels above the 100 lb. rate of applied nitrogen as compared with yield increases with added phosphorus. This relation of nitrogen percentage, phosphorus percentage, and yield indicates a deficiency of phosphorus limited total growth but not uptake of nitrogen at and above the 100 lb. level of applied nitrogen. Otherwise nitrogen deficiency resulting from interspecific competition or a low initial level in the soil or shading by adjacent plants limited growth.

## CONCLUSIONS

Results of this experiment indicated that plant competition was effective through differences in nitrogen uptake by associated plants of the 3 species at or above the 100 lb. level of applied nitrogen. These differences were expressed in total growth with no apparent change in nitrogen percentage when phosphorus was sufficient. They were expressed as changes in nitrogen percentages and minimal changes in total growth when phosphorus was limiting.

When plants of the 3 species were grown monospecifically, availability of soil nitrogen and phosphorus to individual plants constituted the principal factor of competition. There was no indication of differential shading or different total uptake of nitrogen and phosphorus by plants per pot resulting from densities of planting.

Differential ability to take up and utilize soil nitrogen, both under high and low phosphorus regimes, was indicated as the principal factor of competition between the 2 grass species (*B. mollis* and *F. megalura*) grown bi- or trispecifically. Yield data gave no evidence of differential shading resulting from bi- or trispecific competition of these species.

Shading of plants, in combination with differential ability for uptake of nitrogen, appeared most important when plants of *E. botrys* were grown with the grasses, especially at the high level of applied nitrogen. With high nitrogen and high density of planting, leaves of *E. botrys,* which usually grow prostrate or nearly so, were oriented nearly vertically, covered the ground surface, and thus shaded the grass plants growing in the same pot (Figs. 4 and 5). This effect varied with different numbers of plants per pot. Thus, one would suspect that relations among aerial portions of the plants were more effective in competition than were root relations. Also, *E. botrys* strongly suppressed the grasses at the highest level of nitrogen. When the 2 grasses were grown together at the 400 lb. rate of applied nitrogen, increased response of one species was accompanied by little or no decreased response of the associated species.

Another indication of competition for light between the grasses and *E. botrys* at the 400 lb. rate of applied nitrogen is that only in this instance did neither grass species exhibit increased response to increasing nitrogen. Response of *E. botrys* sharply increased at higher levels of nitrogen in this relation.

## Summary

The effects of intra- and interspecific competition at different levels of nitrogen and phosphorus among 3 major species of the annual grassland type of California (*B. mollis, E. botrys,* and *F. megalura*) were studied.

Plants of the 3 species were grown in pots in a greenhouse. Variables of the experiment were intra- and interspecific combinations of planting, densities of planting, and levels of soil nitrogen and phosphorus.

Results indicated that competition was effective through differences in nitrogen uptake by the constituent species. With a high phosphorus level these differences resulted in changes in yield. With low phosphorus they were expressed as differences in nitrogen percentages and minimized yield changes.

Factors of interspecific competition were differential shading and differential ability for uptake of nitrogen. One was more important than the other depending upon the species and species combination.

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# THE ROLE OF FIRE IN ALTERING THE SPECIES COMPOSITION OF FORESTS IN RHODE ISLAND[1]

James H. Brown, Jr.[2]

## Introduction

Fire produces varied effects upon forest sites and forest vegetation itself. In some regions fire is responsible for the widespread occurrence of valuable timber species, and in other regions fire destroys them. In Rhode Island where fire has been a common occurrence for many years, it has been reported that the Indians commonly fired the forests (Bicknell 1920; Day 1953).

Actual research on the effect of fire on vegetation in the United States did not begin until the present century (Chapman 1926, 1932; Heyward 1939; Isaac 1930; Larson 1929; Skutch 1929; Show and Kotok 1924), although reference had been made to fire in many earlier vegetation studies. Studies of the effect of fire on vegetation in areas ecologically similar to Rhode Island have been limited. Nichols (1913), in a study of the vegetation of Connecticut, discussed the effect of fire on the composition of a stand of hemlock, which was severely burned in the eighteenth century, resulting in the elemination of hemlock, with subsequent reversion to chestnut and red oak.

The purpose of this study was to determine what effect fire has had in altering the species composition of woodlands on upland sites in Rhode Island.

## Methods

The upland sites investigated include the forested sections of western Rhode Island that are on well-drained soils of the uplands. Two samples

[1] Contribution No. 972 of the Rhode Island Agricultural Experiment Station, Kingston, Rhode Island.

[2] The author is grateful to Dr. David M. Smith for his helpful suggestions in the preparation of this manuscript.

were taken from neighboring eastern Connecticut.

Sampling areas were selected on the basis of a map, prepared by the Rhode Island Division of Forests (Fig. 1), indicating the areas burned in the past 25 to 30 years. To determine accurate dates of burns and to locate older burned areas, newspapers and the records of the Rhode Island Division of Forests were consulted. On the older less easily recognized burns, it was necessary to examine the area for evidence of fire. Charred chestnut stumps were common on most of these burns, and pieces of charcoal were present within or below the humus layers. Approximate date of the fire was established by determining the age of the present forest cover, since fire typically destroys all of the existing stems except the resistant pitch pine, and the resulting sprouts are even-aged. Only those stands in which fires had been severe enough to kill virtually all hardwood stems were selected for study. Where records were available age of the stands coincided closely with records on time of burning. There was no evidence of more recent lighter fires on the plots examined. However, several of the burned areas had been burned previously in the past 50 years.

Additional areas showing no evidence of having been burned were located and analyzed. The stands, ranging in age from 39 to 108 years, were contrasted with the burned areas. Five of the 9 unburned plots had, at one time, been cleared and either plowed or pastured (Shearin 1957, personal communication), but did not appear to have been burned since reverting to woodland. The unburned plots on "virgin" soils had all been free from fire for a long period—possibly 200 years or more. Topographic features such as rock outcrops, steep slopes, or swamps had apparently served to keep fires out of these stands. Since widespread burning has been reported to have occurred in the past, it would probably be safe to assume that all or the majority of the upland areas had been burned at one time or another. The unburned areas differ from the burned areas in relative time since burning, and severity and frequency of burning. The burned areas in most cases have probably been subjected to repeated fires extending over a long period of time, whereas the areas designated as unburned had been free from fire for a long period of time or as in the case of the old field stands had been free of fire since reversion to woodland.

Two types of samples were used to determine the composition of the vegetation on burned and unburned areas: nested quadrats (Keever 1953),

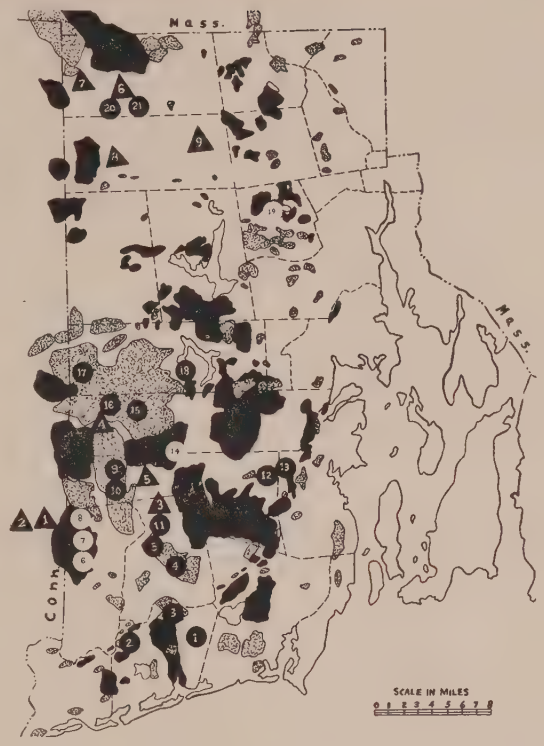


FIG. 1. Rhode Island woodland burned in the period from 1930 to 1940 (solid black area) and from 1940 to 1955 (dotted area). Circles indicate locations of plots in burned stands; triangles indicate locations of plots in unburned stands.

and circular, one-fourth acre plots. Nested quadrats consisted of 10 x 10 meter quadrats from which list counts and diameters of all woody stems over 1 in. dbh were listed by species, and 1 x 1 meter quadrats where counts were made of natural reproduction of tree species. At each sampling point the 10 x 10 meter quadrats were laid out, and the smaller quadrats were nested in the northwest corners except where large boulders or fallen trees interfered. The circular, one-fourth acre plots were established in the summer of 1956 in a survey conducted by the Rhode Island Agricultural Experiment Station, and some of the data collected during this survey were used. The quarter method (Curtis 1956) was used to substantiate data from other methods and did so.

An effort was made to take all of the samples on soils of the Gloucester series, but this was not always possible. Soils of this series are the most common of those derived from glacial tills in southeastern New England. The soil survey manual and maps for Providence county (Shearin *et al.* 1943) and for Kent and Washington counties (Roberts *et al.* 1939) were utilized to determine the soil type for each area. Soil type as well as

other information pecular to each plot is tabulated in Table I.

TABLE I. Soil type, average age of stand and record of previous land use for each burned and unburned area sampled.

| Plot No. | Soil Type | Stand Age, yrs. | Old Field (OF) or "Virgin" (V) |
|---|---|---|---|
| | BURNED AREAS | | |
| 1 | Gloucester stony sandy loam | 41 | V |
| 2 | Gloucester stony fine sandy loam | 11 | V |
| 3 | Gloucester stony fine sandy loam | 13 | V |
| 4 | Hinckley gravelly sandy loam | 5 | V |
| 5 | Narragansett stony fine sandy loam | 5 | V |
| 6 | Gloucester stony fine sandy loam | 29 | V |
| 7 | Gloucester very stony fine sandy loam | 29 | V |
| 8 | Acton fine sandy loam | 29 | OF |
| 9 | Hinckley loamy sand | 6 | V |
| 10 | Hinckley loamy sand | 6 | V |
| 11 | Gloucester stony sandy loam | 34 | V |
| 12 | Narragansett stony silt | 46 | V |
| 13 | Gloucester stony fine sandy loam | 46 | V |
| 14 | Gloucester stony fine sandy loam | 21 | V |
| 15 | Gloucester stony fine sandy loam | 15 | V |
| 16 | Gloucester stony fine sandy loam | 15 | V |
| 17 | Gloucester stony fine sandy loam | 15 | V |
| 18 | Gloucester stony fine sandy loam | 45 | V |
| 19 | Gloucester stony very fine sandy loam | 25 | V |
| 20 | Gloucester stony fine sandy loam | 46 | V |
| 21 | Gloucester stony fine sandy loam | 51 | V |
| | UNBURNED AREAS | | |
| 1 | Shapleigh rocky fine sandy loam | 108 | V |
| 2 | Gloucester fine sandy loam | 62 | OF |
| 3 | Gloucester fine sandy loam | 50 | V |
| 4 | Gloucester stony fine sandy loam | 59 | OF |
| 5 | Gloucester stony fine sandy loam | 50 | OF |
| 6 | Gloucester stony fine sandy loam | 60 | V |
| 7 | Gloucester stony fine sandy loam | 39 | OF |
| 8 | Gloucester fine sandy loam | 54 | OF |
| 9 | Gloucester fine sandy loam | 45 | OF |

Relative density (number of individuals of one species as a percentage of the total number of individuals of all species), and, in case of natural reproduction, frequency (the percentage of quadrats occupied by a species) were calculated for each species by strata class. Basal area and percentage of total basal area were also calculated for the overstory species.

## RESULTS

A total of 21 samples from burned areas was obtained. The most recently burned sites had been burned only 5 years prior to sampling and the oldest 51 years. Nine samples were obtained from unburned areas.

The results will be considered in four categories: overstory, understory, trangressives, and natural reproduction.

### *Overstory Trees*

The overstory is considered to include all vegetation with stems over one inch dbh occurring in the dominant and co-dominant crown classes.

Scarlet oak (*Quercus coccinea*)[3], white oak (*Quercus alba*), and black oak (*Quercus velutina*) are major occupants of both burned and unburned areas (Table II). Density and relative basal area of these three species, however, are greater on burned sites. On burned areas, 90.9 per cent of the stems and 94.88 per cent of the total basal area are of these three species, while on the unburned areas they include only 56.4 per cent of the stems and 53.09 per cent of the total basal area. Red maple (*Acer rubrum*), hemlock (*Tsuga canadensis*) and red oak (*Quercus rubra*) are important species on unburned areas while on the burned sites these species are either present in only small quantities or are absent.

TABLE II. Relative density (D) and percentage of total basal area (BA) of the overstory trees on burned and unburned areas sampled.

| Species | BURNED | | UNBURNED | |
|---|---|---|---|---|
| | (D) % | (BA) % | (D) % | (BA) % |
| *Quercus alba* | 42.7 | 23.40 | 23.6 | 27.60 |
| *Quercus coccinea* | 36.8 | 63.80 | 12.9 | 10.81 |
| *Quercus velutina* | 11.4 | 7.68 | 19.9 | 14.68 |
| *Prunus serotina* | 2.6 | .20 | .3 | .07 |
| *Acer rubrum* | 2.1 | .87 | 10.0 | 3.26 |
| *Quercus rubra* | 1.8 | 3.46 | 14.0 | 21.62 |
| *Quercus ilicifolia* | .9 | .23 | | |
| *Pinus rigida* | .8 | .27 | | |
| *Carya* spp. | .4 | .04 | .7 | .05 |
| *Populus tremuloides* | .2 | .02 | | |
| *Castanea dentata* | .2 | .02 | | |
| *Betula populifolia* | .1 | .02 | 5.4 | .90 |
| *Tsuga canadensis* | | | 6.0 | 12.50 |
| *Pinus strobus* | | | 3.4 | 3.81 |
| *Betula lenta* | | | 1.5 | 4.47 |
| *Betula lutea* | | | 1.3 | .03 |
| *Fagus grandifolia* | | | .8 | .08 |
| *Sassafras albidum* | | | .1 | .09 |
| *Nyssa sylvatica* | | | .1 | .03 |

### *Understory*

The understory includes all vegetation with stems over one inch dbh occurring in the intermediate and overtopped crown classes including potential overstory species and secondary trees and shrubs.

The understory is similar to the overstory on the burned areas in that white oak and scarlet oak are the most numerous species (Table III). But, in the understory a greater percentage of the stems on the burns includes species other than the oaks, especially species of seed origin or slower growing stems of sprout origin.

The unburned areas have a large number of species present in the understory. The oaks are important components of the stands, but other

[3] Nomenclature of species of vascular plants is that of Fernald (1950).

TABLE III. Relative density (D) of the understory trees on burned and unburned areas sampled.

| Species | Burned (D) % | Unburned (D) % |
|---|---|---|
| Potential overstory trees | | |
| *Quercus alba* | 45.3 | 23.8 |
| *Quercus coccinea* | 29.4 | 6.9 |
| *Acer rubrum* | 8.6 | 20.0 |
| *Quercus velutina* | 7.4 | 3.6 |
| *Sassafras albidum* | 2.7 | .3 |
| *Prunus serotina* | 2.4 | .6 |
| *Castanea dentata* | 1.5 | 5.3 |
| *Betula populifolia* | 1.2 | 1.5 |
| *Quercus rubra* | .9 | 2.5 |
| *Pinus strobus* | .3 | 11.9 |
| *Betula lutea* | .3 | 1.5 |
| *Tsuga canadensis* | | 7.9 |
| *Fagus grandifolia* | | 4.7 |
| *Carya* spp. | | 4.5 |
| *Betula lenta* | | 4.2 |
| *Nyssa sylvatica* | | .7 |
| Secondary trees and shrubs | | |
| *Quercus ilicifolia* | 93.4 | 4.2 |
| *Hamamelis virginiana* | 3.1 | 62.3 |
| *Vaccinium atrococcum* | 3.5 | |
| *Kalmia latifolia* | | 14.3 |
| *Ostrya virginiana* | | 9.9 |
| *Carpinus carolinana* | | 5.7 |
| *Cornus florida* | | 3.6 |

species occurring in fewer numbers or nonexistent on burned areas are present or more numerous.

The most numerous species among the secondary trees and shrubs on burned areas is scrub oak (*Quercus ilicifolia*). On the unburned areas witch hazel (*Hamamelis virginiana*) is the most numerous species. Scrub oak is also present, but in fewer numbers. Several other species occur solely on the unburned sites including mountain laural (*Kalmia latifolia*), hophornbeam (*Ostrya virginiana*), bluebeech (*Carpinus caroliniana*), and flowering dogwood (*Cornus florida*).

### *Transgressives*

This portion of the stands includes all woody vegetation below 1 in. dbh, and consists of potential overstory species and secondary trees and shrubs. Only potential overstory species greater than 1 ft. in height were included in the transgressives. Stems less than 1 ft. in height were considered natural reproduction. White oak and scarlet oak are the major occupants of burned areas, with relative densities of 42.4 per cent and 31.9 per cent, respectively (Table IV). Oak species make up a relatively small percentage of the transgressives on unburned sites where red maple, hemlock, yellow birch, black birch, and beech are numerous.

### *Natural Reproduction*

Natural reproduction includes stems of potential overstory species of seed or sprout origin which are less than 1 ft. high.

TABLE IV. Relative density (D) of woody plants from one to ten feet tall (trangressives) found on burned and unburned areas sampled.

| Species | Burned (D) % | Unburned (D) % |
|---|---|---|
| Potential overstory | | |
| *Quercus alba* | 42.4 | 17.0 |
| *Quercus coccinea* | 31.9 | 8.4 |
| *Castanea dentata* | 8.0 | 4.9 |
| *Prunus serotina* | 7.1 | 3.2 |
| *Pinus strobus* | 2.4 | 2.1 |
| *Acer rubrum* | 2.1 | 17.6 |
| *Carya* spp. | 2.1 | 1.8 |
| *Quercus velutina* | 1.4 | 9.0 |
| *Sassafras albidum* | 1.4 | 2.0 |
| *Pinus rigida* | .7 | |
| *Quercus rubra* | .5 | 1.4 |
| *Tsuga canadensis* | | 13.3 |
| *Betula lutea* | | 7.7 |
| *Betula lenta* | | 6.0 |
| *Fagus grandifolia* | | 4.8 |
| *Betula populifolia* | | .5 |
| *Fraxinus americana* | | .2 |
| Secondary trees and shrubs | | |
| *Gaylussacia baccata* | 41.70 | 32.15 |
| *Vaccinium vacillans* | 37.58 | 43.92 |
| *Vaccinium angustifolium* | 11.17 | 1.00 |
| *Comptonia perigrina* | 2.98 | |
| *Quercus ilicifolia* | 2.43 | 2.26 |
| *Myrica pennsylvanica* | .74 | .61 |
| *Kalmia angustifolia* | .68 | 5.03 |
| *Corylus americana* | .58 | .76 |
| *Vaccinium atrococcum* | .41 | 1.58 |
| *Pyrus melanocarpa* | .39 | .57 |
| *Viburnum cassinoides* | .29 | 1.62 |
| *Quercus prinoides* | .29 | .07 |
| *Amelanchier* spp. | .19 | .10 |
| *Kalmia latifolia* | .14 | .68 |
| *Clethra alnifolia* | .14 | 2.79 |
| *Hamamelis virginiana* | .11 | 3.74 |
| *Gaylussacia frondosa* | .09 | .60 |
| *Rhus copallina* | .03 | |
| *Crataegus* sp. | .03 | |
| *Viburnum acerifolium* | | 1.43 |
| *Nemopanthus mucronata* | | .68 |
| *Cornus florida* | | .39 |
| *Viburnum recognitum* | | .01 |

White oak, scarlet oak and chestnut are the most common species in the natural reproduction on burned areas sampled (Table V). The largest frequency values recorded are for white oak and scarlet oak, only 3.3 per cent for each, indicating few seedlings or sprouts in the burned areas.

Unburned areas show more reproduction and a greater number of species with red maple and white oak the most numerous.

Chi-square tests were applied to the basic data for the overstory, potential overstory, and species occurring as natural reproduction, testing the null hypothesis that the proportion of stems of oak species to stems of other species found on burned areas is similar to that on unburned areas (Dixon and Massey 1957). The null hypothesis was

TABLE V. Relative density (D), and frequency (F) of woody plants less than one foot high (natural reproduction) found on burned and unburned areas sampled.

| Species | Burned | | Unburned | |
|---|---|---|---|---|
| | Based on 90 1 x 1 meter plots | | Based on 88 1 x 1 meter plots | |
| | (D) % | (F) % | (D) % | (F) % |
| *Quercus alba* | 42.3 | 3.3 | 28.7 | 18.2 |
| *Quercus coccinea* | 27.0 | 3.3 | 3.8 | 3.4 |
| *Castanea dentata* | 11.5 | 1.1 | | |
| *Quercus rubra* | 7.7 | 2.2 | 7.5 | 4.5 |
| *Pinus strobus* | 3.8 | 1.1 | 3.8 | 3.4 |
| *Quercus velutina* | 3.8 | 1.1 | 5.0 | 4.5 |
| *Sassafras albidum* | 3.8 | 1.1 | | |
| *Acer rubrum* | | | 30.0 | 12.5 |
| *Tsuga canadensis* | | | 8.7 | 3.4 |
| *Carya* spp. | | | 5.0 | 2.3 |
| *Prunus serotina* | | | 3.8 | 1.1 |
| *Fagus grandifolia* | | | 2.5 | 2.3 |
| *Betula lutea* | | | 1.2 | 1.1 |

proved false in each case. In all cases P was less than .001 indicating that the probability of encountering as large or larger values of Chi-square due to chance is less than 1 time out of 1000. This shows a significant difference in species composition between burned and unburned areas with respect to proportion of oak to non-oak stems.

## Discussion

There is a difference in species composition between burned areas and unburned areas in western Rhode Island. The tolerant species and those reproducing by seed are eliminated or greatly reduced by fires, including hemlock, beech, yellow birch, black birch and white pine. Typically, sprouting species including black oak, scarlet oak and white oak are the major occupants of burned areas. Pitch pine was noted to be abundant on burns in several localities on the extremely drouthy soils. Species found in limited numbers include red oak, black cherry, hickory, chestnut, red maple, white pine, gray birch, sassafras and poplar. Light seeded species were scarce even on the recently burned areas. This could be attributed to the seasonal timing of fires, since most fires occur in the spring at a time when seed is not available for dispersal. The only species with ripe seed at this time are the poplars, but they too were poorly represented on burned areas. This was attributed to the relatively small area of exposed mineral soil available for seedling establishment, even where fire had been severe enough to kill all of the former stand. Poplar and gray birch were noted to be common only on the outer edges of burns where fire had burned up to open fields or roads. White pine, although very scarce on the burned areas examined, was noted to be numerous on burns where large white pines escaped destruction and could thus serve as seed trees. An influx of the light-seeded tolerant species was apparent only where the burns were adjacent to unburned areas containing these species. In one instance on a 46 year old burned area, several yellow birch had apparently seeded in from a nearby swamp. The length of time for any significant invasion of the species eliminated by fire depends upon seed source, severity and frequency of fire, size of area burned, and the condition of the site. There was no relationship between composition and time since fire on the burned plots. It appears that the species composition of burned areas will remain predominantely oak indefinitely.

The possibility that the unburned stands were much better or moister sites than those of the burned stands was considered. Favorable moisture conditions associated with good sites might tend to resist fire, while poor sites due to lack of moisture would be more subject to fire. If this were true, one would be comparing different sites more than differences in history of burning. To counter this possibility site indices were calculated for the unburned plots, and for the burned plots taken in stands over twenty years old. The height curves of Schnur (1937) for even-aged upland oak forests were used as a basis for the calculation of the site indices. Site indices for the unburned plots had an average of 55.4 and ranged from a low of 42 to a high of 65. The average for burned plots was 51.4 and ranged from 44 to 60. These differences were considered negligible and the sites were considered to be, in the aggregate, similar. Any changes in site indices resulting from burning were assumed to be negligible.

Those sprouting species characterized by relatively slow growth have greater proportions of stems in the subordinate strata than in the overstory. Little (1938) found that white oak has more, but shorter, sprouts per stump than do black oak and scarlet oak. Before the 14th year height is greatest for scarlet oak followed by black oak, but persistence of sprouts runs in the order: white, black and scarlet. This partly explains why white oak has large percentages of stems occurring as understory and as transgressives, and also why the fast growing sprouts of scarlet oak and black oak are relatively more numerous in the overstory. White oak is intermediate in light tolerance and is capable of remaining vigorous for prolonged periods under a forest canopy (Kramer, Oosting and Korstian 1952; Minckler

1957), and thus will likely make up large proportions of the understory and overstory in the future. To a limited extent this applies also to red oak, which is able to survive for long periods under poor light conditions (Scholz 1955), but which requires more moisture for optimum growth (Korstian 1927). The moisture requirement will limit red oak to the better sites. Scarlet oak and black oak are less tolerant than white oak and usually perish unless in the upper crown classes. Evidently, the composition of burned areas will remain primarily oak for an indefinite period of time, but with a greater proportion of white oak, and on the better sites red oak.

While oaks are abundant on burned areas; they are also abundant on unburned areas. This prevalence of oak is apparently the result of a long history of disturbance which has tended to favor the intolerant sprouting species. White oak and red maple will apparently continue to make up large proportions of the stands on unburned areas with white pine and hickory also undoubtedly present, while black oak and scarlet oak evidenced by the small number of stems in the smaller size classes will be scarce in future stands. Red oak, hemlock, beech, black birch and yellow birch will likely be present in the overstory in greater numbers.

## Summary

Burned areas were compared with unburned areas to determine the effect of fire on the species composition of woodlands on upland sites in Rhode Island. In 1956 and 1957 samples were obtained from burned areas ranging from 5 years to 51 years since burning, and from areas showing no sign of having been burned.

Fire has altered species composition of the upland forest in Rhode Island. The tolerant species and the species reproducing by seed have been greatly reduced by fires. The intolerant sprouting species capable of surviving fires, including white oak (*Quercus alba*), scarlet oak (*Quercus coccinea*) and black oak (*Quercus velutina*), are the major occupants of burned areas. These three species make up the major proportion of stems in all size classes indicating that the species composition will remain oak indefinitely.

The oaks are important constituents of unburned stands, but other species including white pine (*Pinus strobus*), hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), black birch (*Betula lenta*) and yellow birch (*Betula lutea*) generally occur in all size classes. It is likely that in future stands these species will be present in the overstory in greater numbers.

The prevalence of oak both in burned as well as unburned stands is apparently the result of a long history of disturbance and burning.

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# A PHYTOSOCIOLOGICAL STUDY OF A SMALL PRAIRIE IN WISCONSIN

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Two general approaches to the study of vegetation are in common use: the extensive approach in which a large number of stands is sampled by relatively rapid survey methods (Hanson and Whitman 1938; Curtis and McIntosh 1951) and the intensive approach in which much of an investigation is spent in a detailed evaluation of a comparatively small area (Steiger 1930). There is much to recommend each approach, but the latter is of particular value when it follows a more extensive survey and when it is possible to evaluate results of local study in terms of the inter-stand variability brought to light with extensive survey methods.

The prairies of Wisconsin have been subjects of a number of phytosociological studies, both extensive and intensive, in the last decade. Curtis and Greene (1949) studied 67 relic prairie areas on a wide variety of topographic situations throughout southern Wisconsin, and Curtis (1955) subsequently analyzed the phytosociological behavior patterns of prairie species based on presence data from 157 stands located in 37 counties of the State. These researches have shown that while the prairies of Wisconsin may for convenience be segregated into topographic types (wet, mesic, and dry), the types are not discrete but grade imperceptibly from one to the other as moisture conditions change with topographic position. Curtis (1955) has outlined a prairie continuum for the state in which the dominants are from wet to dry topographic situations, *Calamagrotis canadensis, Spartina pectinata, Sorghastrum nutans, Stipa spartea, Sporobolus heterolepis, Andropogon scoparius* and *Bouteloua curtipendula. Andropogon gerardi* is the most important single species on Wisconsin praries and occurs as a dominant in all prairie types.

A number of less extensive studies have been made on prairies within local areas or on those occurring within a narrow range of topographic positions. Green (1950) analyzed the floristic composition of 5 mesic prairie remnants on well-drained silt-loam soils in Rock County, while Whitford (1958) has studied 27 remnants of the Racine-Kenosha clay prairies of southeastern Wisconsin. The floristic composition and soil characteristics of the dry-lime prairies of southern Wisconsin have been studied by Anderson (1954). Dix and Butler (1954) have evaluated the effects of fire on these grasslands and Dix (1959) has reported their deterioration under livestock grazing. Correlations between soil characteristics and species composition on a mesic to wet prairie in Jefferson County have been evaluated by Partch (1949), and Bray (1956) has reported the mutual occurrence of plant species on mesic prairies along the Mississippi River. Prior to our study, no detailed phytosociological analysis had been made of a mesic-dry prairie in Wisconsin.

This study was initiated (1) to determine the phytosociological interrelationships between plant species on a small prairie area towards the dry end of the prairie gradient in Wisconsin, (2) to investigate environmental factors which determine or influence these interrelationships, and (3) to compare the behavioral patterns of species on a small area with behavior against similar phytosociological and environmental gradients over a wide geographical area.

## METHODS

In choosing a site for the study, it was necessary to select an area with enough environmental heterogeneity to permit some diversity in species composition. It seemed equally desirable to have the environmental heterogeneity within an area small enough to allow each set of environmental measurements (e.g., soil moistures, surface temperatures) to be recorded within a period which

would insure their reliability in comparative studies within the prairie. The site selected is 3 miles southwest of Lodi, Wisconsin on the boundary line separating Dane and Columbia Counties (SW ¼ Sec. 32, T. 10 N., R. 8E.). According to its owner, this 2.5 acre prairie had been neither grazed nor burned for 25 years and there was no evidence of disturbance or fire at the time of the study. Underlying bedrock, which outcrops at several locations on the prairie, is of Lower Magnesian Dolomite. The soil, which is uniform over the entire prairie, is a fertile silt-loam; 4 soil samples, collected from widely separated locations, showed the following averages for soil nutrients in available pounds per acre: calcium 8,375, magnesium 850, potassium 200, phosphorus 87.5, nitrate 4.5, and ammonia 12.5. The pH values varied from 7.5 to 8.0 The climate is continental with long cold winters and short warm summers; average annual precipitation is approximately 31 in.

The study area was surveyed with a surveyor's transit; a topographic map of the site is shown in Figure 1. A grid system was established on the prairie so that each line was 20 ft. from its nearest parallel neighbor and a $m^2$ quadrat was placed at each intersection of the grid lines. The presence of species was recorded in 250 such quadrats.

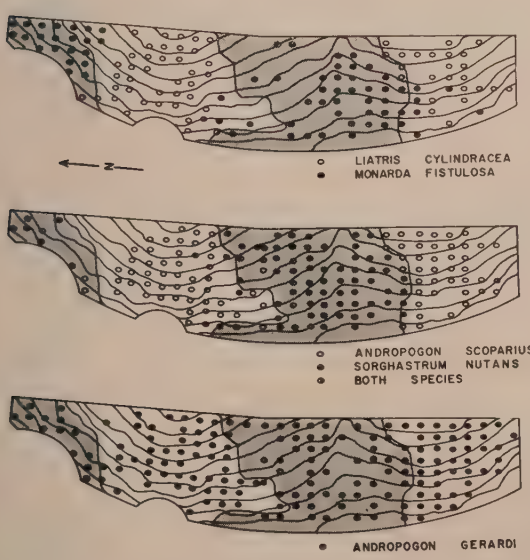


FIG. 1. The mapped occurrences of selected species on the prairie. Each circle represents the occurrence of the indicated species in the quadrat at that location. The stippled area represents soil depths equal to or greater than 4 inches while clear areas indicate soil depths of less than 4 inches. The contour intervals are 5 feet while the distances between the quadrats are 20 feet.

Environmental measurements were also made in each quadrat. Soil depth of each quadrat was obtained by averaging 5 measured probe distances to the bedrock. Soil moistures were measured by collecting approximately 200 g of soil at a depth of 1-3 in. from 3 locations within each quadrat, pooling the 3 sub-samples into a paper bag and immediately placing the bag in a small box to minimize water loss to the atmosphere. After a few (usually 5 or 6) samples had been taken from adjacent quadrats, they were carried to a weighing station nearby and weighed to the nearest 0.1 g on a triple-beam balance. Preliminary experiments had shown that moisture lost between collection and field weighing was not measurable within limits of $\pm 0.1$ g when the field weight was made within 10 minutes of collection. The weighing stations were frequently moved over the prairie as sampling progressed to keep the time intervals within the 10 minute period. After the field weighing, soil samples were taken to the laboratory, oven-dried at 105°C for 72 hr., reweighed and the soil moistures were calculated in per cent on a dry weight basis. All samples for soil moisture determinations were collected on August 31 and September 1, 1953 between 11:00 and 15:30 hr. These dates were chosen because of the paucity of precipitation in the preceding weeks. Total precipitation for the 27 day period preceding sampling, as recorded by the weather station at Prairie du Sac, was as follows: Aug. 4, 1.17 in., August 8, .34 in., and August 11, .17 in. This method of obtaining soil moisture data was selected on the assumption that the effectiveness of soil moisture as a limiting factor for plant growth would be most pronounced during periods of prolonged drought.

Surface soil temperatures were measured in degrees Fahrenheit with ordinary mercury-bulb thermometers. One thermometer was placed in the deepest shade in each quadrat. Subsurface temperatures were measured by commercial mercury-bulb soil thermometers. Each thermometer was encased in a wooden frame with a thin, cone-shaped copper covering to protect it when inserted in the soil. Soil thermometers were inserted 2 in. in the soil in the deepest shade in each quadrat. One surface and one sub-surface measurement was made in each quadrat. Temperature data so obtained were found to be reproducible within $\pm 2$°F and therefore appear satisfactory for comparative studies within the prairie. All temperature measurements were made on September 2, 1953 between 12:00 and 15:00 hr. and are considered directly comparable. On that day, the sky was

virtually cloudless and the maximum temperature recorded at the Prairie du Sac weather station was 95°F while an air temperature of 98°F was recorded in full shade 4 ft. above the soil surface on the prairie. This discrepancy is not surprising since several weather stations nearby recorded 99°-100°F maximum temperatures for the day. The water-retaining capacities of the soils were obtained by the standard Hilgard-cup method.

The possibility that soil nutrients play a significant role in determining or influencing species distributions on this prairie seems remote. Previous work by Anderson (1954), Curtis (1955) and Dix (1959) failed to show correlations between species distributional patterns and soil nutrient levels on Wisconsin prairies. In view of this, the expense of soil analyses appeared unjustified in the present study. The consistent absence of such correlations has been interpreted to mean that soil nutrients exist on Wisconsin prairies in amounts large enough for nearly optimum growth of all important species of the prairie flora (Dix 1955).

Final data for the quadrats were recorded on punch cards—one card for each quadrat. The presence or absence of each of the 42 most common species was recorded on each card. The range of values for each environmental factor was divided into 4 value levels and the appropriate values indicated on each card. By this method, it was relatively simple to compare the occurrence of any one species with the occurrence of any other species or with any one of the several environmental factors by sorting the cards in various ways. The prairie was divided into 25 plots to facilitate its study at the community level; each plot consisted of 10 contiguous quadrats. A special data form was prepared with the names of the 42 common species listed alphabetically in a single column along one edge of the page and blanks were provided for recording the environmental values. Each plot was represented by one form; each form contained the frequency value (per cent of occurrence of a species in the 10 quadrats of the plot) for each of the 42 common species and the final environmental values, also averaged from 10 quadrats. Again, it was relatively simple to compare the species composition and the environmental value levels between plots by sorting the forms in various ways.

Taxonomic nomenclature is according to Fernald (1950).

TABLE I. Comparisons of the total number of plant families, total number of plant species and the percentage of species contributed to the flora by four major families on Wisconsin and Nebraska prairies.

| | Total No. of Families | Total No. of Species | Plant Families: Percents of Species in Four Families | | | |
|---|---|---|---|---|---|---|
| | | | Compositae | Gramineae | Leguminosae | Asclepiadaceae |
| Lodi Prairie | 34 | 101 | 30 | 15 | 4 | 4 |
| Whitford (1958) | 45 | 173 | 25 | 8 | 8 | 4 |
| Green (1950) | 36 | 108 | 31 | 11 | 11 | — |
| Curtis and Greene (1949) | 52 | 237 | 27 | 10 | 7 | 4 |
| Steiger[1] (1930) | 59 | 237 | 20 | 16 | 8 | 5 |

[1] *Cyperaceae* contained an additional 8% of the species, but this family was not highly represented in any other study.

## RESULTS

### *Family Composition Study*

A total of 101 species of vascular plants, representing 76 genera and 34 families, was found on the prairie. Thirty per cent belonged to the *Compositae,* while the *Gramineae, Leguminosae,* and *Asclepiadaceae* were represented by 15%, 4% and 4% of the species, respectively. When these figures were compared to those of other studies (Table I) of Wisconsin prairies, both local and general (Green 1950; Whitford 1958; and Curtis and Greene 1949), remarkable similarities were evident. These indicated that the 4 major plant families contributed approximately ½ the species on Wisconsin prairies, regardless of topographic position or soil texture of the site. Thus, family composition similar to that of our mesic-dry prairie was found in prairies occupying heavy mesic-wet clay soils (Whitford), mesic silt-loam soils (Green), and in a composite presence list from 65 stations occupying a wide variety of topographic positions and soil textural types in Southern Wisconsin (Curtis and Greene). Furthermore, the relative importance of each of these plant families appeared remarkably constant whether the areas sampled were distributed over a few acres, as in this study, a few hundred square miles, as in the studies of Whitford and Green, or thousands of square miles, as in the study of Curtis and Greene. This suggests that while various topographic positions and soil textural types support different species composition (Curtis 1955), the majority of component species are derived from only 4 plant families. Thus, the floristic composition of Wisconsin prairies appears relatively constant at the family level but highly variable at the species level. A similar family composition reported by Steiger (1930) for a mile-square tall-grass prairie near Lincoln, Nebraska (Table I), showed that dominance of these 4 plant families also occurs in other areas of the North American Prairie and suggests that the

TABLE II. Coefficient of community values for the 25 plots of the Lodi Prairie. The values given in the body of the table represent vegetational similarities between the plots. The plots are arranged in such a way that those with high similarities are close together while those with low similarities are far apart. The obtained ordination of plots is divided into four groups—three groups contain 6 plots and one group contains 7 plots.

| Groups | | 1 | | | | | | 2 | | | | | | 3 | | | | | | 4 | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Plots | 18 | 11 | 13 | 12 | 4 | 17 | 3 | 2 | 19 | 24 | 20 | 25 | 5 | 1 | 14 | 10 | 8 | 9 | 7 | 21 | 15 | 16 | 22 | 23 | 6 |
| 1 | 18 | — | 78 | 73 | 75 | 60 | 72 | 70 | 65 | 57 | 49 | 39 | 44 | 67 | 39 | 39 | 33 | 32 | 27 | 29 | 33 | 32 | 30 | 24 | 17 | 12 |
| | 11 | | — | 72 | 74 | 65 | 64 | 71 | 77 | 66 | 55 | 47 | 26 | 46 | 48 | 44 | 41 | 35 | 34 | 35 | 36 | 38 | 35 | 27 | 20 | 17 |
| | 13 | | | — | 75 | 56 | 70 | 61 | 62 | 56 | 45 | 49 | 43 | 40 | 37 | 44 | 29 | 28 | 28 | 27 | 31 | 41 | 35 | 23 | 25 | 14 |
| | 12 | | | | — | 57 | 69 | 56 | 63 | 56 | 49 | 49 | 40 | 39 | 36 | 46 | 19 | 32 | 28 | 32 | 33 | 36 | 36 | 25 | 20 | 17 |
| | 4 | | | | | — | 54 | 76 | 71 | 73 | 67 | 62 | 66 | 64 | 59 | 57 | 56 | 56 | 53 | 54 | 54 | 43 | 43 | 43 | 45 | 56 |
| | 17 | | | | | | — | 60 | 58 | 59 | 50 | 50 | 51 | 46 | 46 | 47 | 39 | 32 | 38 | 31 | 37 | 37 | 30 | 30 | 23 | 18 |
| 2 | 3 | | | | | | | — | 75 | 69 | 55 | 54 | 62 | 56 | 57 | 46 | 50 | 46 | 48 | 44 | 49 | 40 | 37 | 33 | 32 | 28 |
| | 2 | | | | | | | | — | 64 | 67 | 48 | 61 | 48 | 53 | 45 | 44 | 42 | 40 | 47 | 37 | 39 | 38 | 32 | 30 | 21 |
| | 19 | | | | | | | | | — | 66 | 66 | 70 | 67 | 59 | 61 | 61 | 60 | 60 | 54 | 64 | 50 | 48 | 49 | 50 | 41 |
| | 24 | | | | | | | | | | — | 64 | 65 | 65 | 57 | 56 | 50 | 54 | 54 | 58 | 58 | 50 | 53 | 53 | 56 | 39 |
| | 20 | | | | | | | | | | | — | 68 | 68 | 66 | 62 | 64 | 55 | 68 | 57 | 60 | 46 | 43 | 47 | 50 | 44 |
| | 25 | | | | | | | | | | | | — | 65 | 81 | 58 | 57 | 58 | 56 | 55 | 56 | 46 | 38 | 49 | 50 | 41 |
| 3 | 5 | | | | | | | | | | | | | — | 63 | 57 | 69 | 72 | 68 | 66 | 71 | 49 | 56 | 59 | 62 | 59 |
| | 1 | | | | | | | | | | | | | | — | 60 | 65 | 55 | 59 | 57 | 59 | 46 | 41 | 48 | 56 | 48 |
| | 14 | | | | | | | | | | | | | | | — | 55 | 46 | 56 | 51 | 51 | 68 | 51 | 44 | 42 | 44 |
| | 10 | | | | | | | | | | | | | | | | — | 66 | 76 | 60 | 66 | 42 | 40 | 50 | 52 | 56 |
| | 8 | | | | | | | | | | | | | | | | | — | 64 | 76 | 70 | 47 | 55 | 59 | 52 | 59 |
| | 9 | | | | | | | | | | | | | | | | | | — | 59 | 40 | 50 | 49 | 37 | 50 | 52 |
| 4 | 7 | | | | | | | | | | | | | | | | | | | — | 66 | 44 | 61 | 65 | 70 | 62 |
| | 21 | | | | | | | | | | | | | | | | | | | | — | 43 | 54 | 60 | 59 | 56 |
| | 15 | | | | | | | | | | | | | | | | | | | | | — | 68 | 49 | 45 | 45 |
| | 16 | | | | | | | | | | | | | | | | | | | | | | — | 50 | 57 | 47 |
| | 22 | | | | | | | | | | | | | | | | | | | | | | | — | 67 | 67 |
| | 23 | | | | | | | | | | | | | | | | | | | | | | | | — | 79 |
| | 6 | | | | | | | | | | | | | | | | | | | | | | | | | — |

phenomenon may be characteristic of the entire prairie region. The ecological and phytogeographical significance of the dominance of these families is not yet clear, but further investigations along these lines appear to hold great interest.

### *Community Study*

The next approach to the analysis of the vegetation was at the communal level. To reduce the volume of the data, the prairie was divided into 25 plots as described above. To evaluate the phytosociological relationships between the plots, they were ordered by an application of a coefficient of similarity index. Similarity coefficients were found by the formula

$$K = \frac{2w}{a + b} \times 100$$

where K is the coefficient of similarity between 2 plots (A and B), a and b are the sums of frequencies for all species in plots A and B respectively, and w is the sum of frequencies shared by the 2 plots. According to this formula, K= 100 when the 2 plots have exactly the same species composition and K=0 when 2 plots have no species in common.

The ordination matrix of the plots is presented in Table II. This ordination attempted to place those plots with the greatest similarities closest together and those with least similarities farthest apart. Thus, plots 18 and 11 are interpreted to be most similar while plots 18 and 6 are interpreted to be least similar plots. The position of plots was arrived at by an inspection process which attempted to place the highest coefficient values along the hypotenuse and the lowest towards the upper right corner of the triangular matrix. It can be seen from the patterns of interchange between various plots that the magnitude of the similarity coefficients, as compared with plot 18, decreases in a relatively orderly manner from left to right across the top line of the matrix. Similarly, the coefficients, as compared to plot 6, increase from top to bottom along the right edge and from right to left across the top line of the matrix. The patterns of the relationships between other plots are also evident.

To determine the behavior of individual species along the ordination of plots, the ordination in Table II was divided into 4 groups containing 6, 6, 6, and 7 plots each, and the frequencies of each species in each group were averaged. A list (Table III) was then prepared so that those species with

the greatest values in Group I (plots 18-17) were placed at the top and those species with the greatest values in Group IV (plots 7-6) were placed at the bottom of the column. It is evident from Table III that most species exhibit Gaussian distributions along the gradient, although there are some irregularities in those with relatively low average frequency values and in ubiquitous species such as *Andropogon gerardi*.

Causes for the distributional patterns in Table III are suggested by data for edaphic factors in Table IV. Plot groups in Table IV are the same as in Table III. Figures in the table were obtained by averaging the edaphic measurements in the plots. Each edaphic factor, with the possible exception of the water-retaining capacity, exhibits a distinct gradient along the plot ordination (Table IV). The nature of these correlations will be treated below.

Although this coefficient of similarity index proved effective for objectively ordering the plots, it did not demonstrate the phytosociological distances (degree of compositional similarity and dissimilarity) between them. It seemed desirable, therefore, to employ some additional method which would indicate the spatial position of each plot on a second ordination and, in this way, measure the ecological distance between plots. Accordingly, the technique of assigning numerical adaptation values to selected indicator species was applied. Ten indicator species from the list in Table III were assigned adaptation numbers from 1 to 5 on the basis of their occurrences within the Groups. Species with the greatest preference for Group I received adaptation numbers of 1, species with the least preference for Group I received adaptation numbers of 5, while those with intermediate preferences received intermediate adaptation numbers. The adaptation numbers of the indicator species are given in Table III.

Plot Index Values (P.I.V.) for the 25 plots were found by applying the formula

$$\text{P.I.V.} = \frac{\text{Sum (Relative frequency of each indicator species X its adaptation number)}}{\text{Sum (Relative frequency for each indicator species)}}$$

Frequency index values in each plot were converted to relative frequency values to impart definite numerical limits to the ordination. Under this system, a plot will have a P.I.V. of 1 when it contains only indicator species with adaptation numbers of 1. Similarly, P.I.V.'s of 5 are obtained when all indicator species present have adaptation numbers of 5, while plots containing a mixture of indicator species will have intermediate P.I.V.'s. This second ordination (Fig. 2) was established by placing the P.I.V.'s so that each plot had a linear spatial relationship to each of its associates. The behavior of a few selected species against the

TABLE III. Average frequency values in four groups of plots for all species[1] which occurred in ten or more quadrats. The ordination in Table II was divided into four units containing 6,6,6, and 7 stands and the frequencies of each species in each group averaged. The listing of species in this table attempts to place those species with the greatest affinity for groups 1 and 4 at the top and bottom, respectively. Numbers to the left of the species names are the adaptation values assigned to the ten indicator species.

| | GROUPS | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| 1. Liatris cylindracea | 65 | 33 | 10 | — |
| 1. Panicum prelongum | 32 | 8 | 3 | — |
| Solidago nemoralis | 35 | 12 | 3 | 1 |
| Viola pedata | 38 | 18 | 7 | 9 |
| Antennaria spp. | 17 | — | 3 | — |
| Aster linariifolius | 30 | 12 | 2 | — |
| Petalostemum purpureum | 15 | 13 | — | — |
| Bouteloua curtipendula | 72 | 71 | 32 | 15 |
| 2. Andropogon scoparius | 80 | 62 | 20 | 6 |
| 2. Aster sericeus | 62 | 28 | 25 | 10 |
| Sporobolus heterolepis | 58 | 32 | 18 | 7 |
| Aster azureus | 82 | 53 | 23 | 32 |
| Carex pensylvanica | 20 | 8 | 6 | 4 |
| Andropogon gerardi | 72 | 78 | 52 | 72 |
| Melilotus spp. | 6 | 25 | 8 | 5 |
| Aster ptarmicoides | — | 16 | — | — |
| Solidago rigida | 8 | 8 | 3 | 1 |
| Convolvulus arvensis | — | 18 | 5 | 4 |
| Anemone cylindrica | 3 | 10 | 7 | 1 |
| Coreopsis palmata | 8 | 35 | 20 | 21 |
| Solidago speciosa | 12 | 8 | 13 | 11 |
| Potentilla arguta | 15 | 10 | 10 | 11 |
| Physalis heterophylla | 2 | 3 | 9 | 6 |
| Prunus serotina | 10 | 5 | 6 | 16 |
| Kuhnia eupatoroides | 7 | 23 | 17 | 10 |
| Ratibida pinnata | 12 | 12 | 9 | 26 |
| Panicum oligosanthes | 10 | 15 | 9 | 4 |
| Euphorbia corollata | 30 | 72 | 70 | 60 |
| Populus tremuloides | 10 | — | 13 | 17 |
| 3. Amorpha canescens | 23 | 57 | 75 | 32 |
| 3. Panicum leibergii | 5 | 21 | 55 | 10 |
| Aster ericoides | 3 | 1 | 8 | 17 |
| Stipa spartea | 10 | 2 | 6 | 10 |
| Poa pratensis | 27 | 55 | 83 | 86 |
| Vitis vulpina | — | 2 | 9 | 9 |
| Equisetum kansanum | 5 | — | 2 | 18 |
| Prysalis virginiana | 3 | 21 | 16 | 27 |
| Rosa sp. | 3 | 5 | 16 | 37 |
| 4. Sorghastrum nutans | 3 | 15 | 28 | 67 |
| 4. Monarda fistulosa | 3 | 17 | 18 | 65 |
| 5. Desmodium illinoense | — | — | 7 | 10 |
| 5. Asclepias syriaca | — | — | 2 | 18 |

[1] *Antennaria* spp. and *Rosa* sp. represent plants whose taxonomy in this area has not been clearly established. *Melilotus* spp. = *M. alba* and *M. officinalis*.

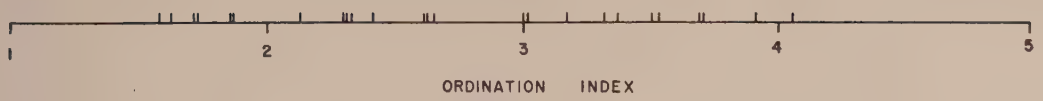


FIG. 2. The plot index ordination (second ordination). The linear arrangement of the 25 plots is according to their Plot Index Values.

TABLE IV. Average values for edaphic factors in the four plot groups. The plot groups are the same as in Tables II and III. The extreme values for each factor are given in the two righthand columns.

| | Plot Groups | | | | Extremes | |
|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Maximum | Minimum |
| Soil Depths, inches | 2.0 | 2.9 | 8.3 | 11.0 | 40+ | 0 |
| Soil Moistures, per cent. | 5.9 | 6.0 | 10.3 | 14.5 | 33 | 2 |
| Soil Temperatures, °F | | | | | | |
| Surface | 109.9 | 104.1 | 95.5 | 87.1 | 124 | 72 |
| 2" below surface | 96.1 | 94.2 | 88.2 | 83.8 | 110 | 72 |
| Water-Retaining Capacities, per cent. | 60.0 | 61.0 | 63.7 | 65.0 | 75 | 43 |

second ordination is shown in Figure 3. To compare the second ordination with the original (Table II), the second was divided into 4 equal segments, as had been done with the original, and frequency values for each species in each segment were averaged. Behavior patterns of the species in the 4 new groups were remarkably similar to patterns in the original groups (Table III) and are not presented. A test for rank correlation (Snedecor 1956) was also used to compare the 2 ordinations; they were correlated at the one per cent level of significance. The data for edaphaic factors were also averaged within the 4 new groups and were similar to the figures in Table IV. The spatial relationships of the plots in Figure 2 are interpreted to indicate that the phytosociological gradient existing on this prairie is gradual and continuous. Were this not so, the location of plots on the second ordination (Fig. 2) would have shown a more aggregated distribution.

### *Environmental Correlations*

Since behavior patterns of species along phytosociological ordinations do not, in themselves, demonstrate causative agents, the environmental data were examined to determine the factor or factors influencing the distributional patterns. Data had been collected on the water-retaining capicity of $A_0$ soil horizon, soil moisture, soil depth and temperatures at the soil surface and at 2 in. below the surface.

Previous work on Wisconsin prairies by Partch (1949) and Curtis (1955) had shown the phytosociological behavior patterns of many species were strongly correlated with the water-retaining capacity of the soil, so first attention was given

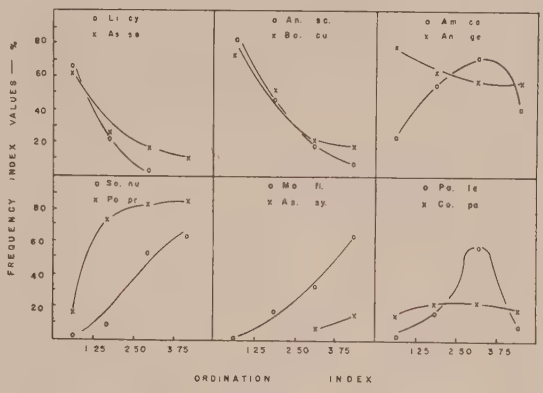


FIG. 3. The phytosociological behavior of selected species against the plot index ordination. Thin-soil plots are towards the left and deeper soil plots are towards the right along the ordination.
The species are:
Upper row, from left to right
Li. cy. = *Liatris cylindracea*
As. se. = *Aster sericeus*
An. sc. = *Andropogon scoparius*
Bo. cu. = *Bouteloua curtipendula*
Am. ca. = *Amorpha canescens*
An. ge. = *Andropogon gerardi*
Lower row, from left to right
So. nu. = *Sorghastrum nutans*
Po. pr. = *Poa pratensis*
Mo. fi. = *Monarda fistulosa*
As. sy. = *Asclepias syriaca*
Pa. le. = *Panicum leibergii*
Co. pa. = *Coreopsis palmata*

to this factor. Although some slight correlation between the plot ordination in Table III and water-retaining capacity is suggested in Table IV, no correlations could be demonstrated when mean water-retaining capacities for the individual plots were plotted against the first (Table II) and the second (Fig. 2) ordinations. Attempts were made to correlate the behavior of individual species with the water-retaining capacity values from individual quadrats. These comparisons were made by dividing the water-retaining capacities from the quadrats into 3 size classes (43-52, 53-62 and 63-72%) and determining the percentage of occurrence of each species in each class. No significant correlations were found. The water-retaining capacities of these soils varied only from 43-75% (mean, 62%) and it was concluded that these differences were not great enough to account for the distributional patterns of the plants.

As a further step, data for soil depths, soil moistures, surface temperatures and subsurface temperatures were averaged by plots and plotted against the stand ordination in Figure 2. Positive correlations with the ordination were found for soil depths and soil moistures while negative correlations were found for surface and sub-surface temperatures. One example of these correlations is illustrated in Fig. 4. To test these correlations, Chi squares were calculated for mutual occurrence of either high or low values for each edaphic factor with each of the other edaphic factors. It was determined that: 1) high soil depths (i.e., deep soils) and high soil moistures were positively associated; 2) low soil depths and low soil moistures were positively associated; 3) high surface and high sub-surface temperatures were positively associated; 4) low surface and low sub-surface temperatures were positively associated; 5) both high soil depths and high soil moistures were negatively associated with high surface and high sub-surface temperatures; and 6) both low soil depths and low soil moistures were negatively associated with low surface and sub-surface temperatures, all at the 5% level. Thus, it seems clear that the edaphic factors are not independent variables along the stand ordination.

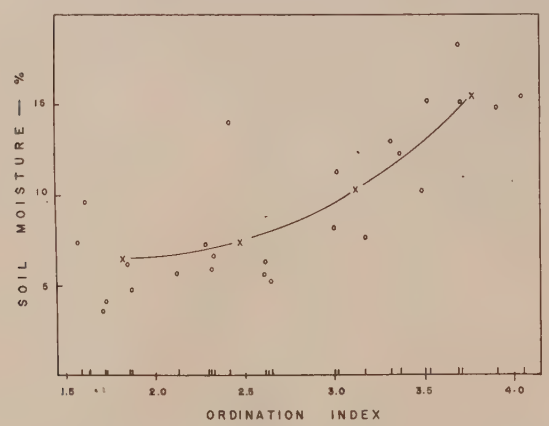


FIG. 4. The occurrence of soil moisture values along the plot index ordination. The marks along the base line represent the location of the plots on the ordination (Fig. 2). Soil moisture values for the plots are indicated by an "o" while the averages of the plots within 1.0 intervals are represented by an "x".

To determine which of the edaphic factors might demonstrate the best correlation with the vegetation, the value for each edaphic factor in each quadrat and the presence or absence in each quadrat of each of the 42 most common species were placed on punch cards; each quadrat was represented by a single card. Thus, an analysis of the data was made independently of the plot ordinations established above. The range of values for each edaphic factor was divided into 4 parts and the percentage of occurrence of each species in each part of the environmental range was determined by sorting the cards into 4 value-level groups. An example of this procedure is given in Table V. Soil depths were segregated on a geometric progression series (0-2.0, 2.0-4.0, 4.0-8.0, and 8.0+ in.) and the percentage of occurrence of each species in each group was determined. Thus, *Aster ptarmicoides* occurred in 11% of the 38 quadrats which had a soil depth between 0 and 2.0 in. The frequency distribution patterns in Table V again demonstrated Gaussian distribution. When punch cards were segregated on the basis of 4 value-level groups for soil moistures, surface temperatures and sub-surface temperatures, similar distributional patterns were obtained, although, in each case, a slightly greater number of irregularities was apparent. The behavior of edaphic factors along the soil-depth gradient is given in Table VI. Because of strong correlations between the edaphic factors, the behavior of any species in Table V along any of the edaphic gradients in Table VI can be predicted with accuracy. For example, frequency values for *Liatris cylindracea* are inversely proportional to soil moistures and directly proportional to surface and sub-surface temperatures. Again, water-retaining capacities showed no correlation with other edaphic factors or with species distribution.

When plant heights were plotted (Fig. 5) against the ordination index shown in Figure 2 and the resultant behavioral pattern compared to the behavioral patterns for soil depths, soil moistures, and surface and sub-surface temperatures, heights were found to be postively correlated with soil depths and soil moistures and negatively correlated with surface and sub-surface temperatures.

While the distribution of plant species in this study have been shown to be strongly correlated with a number of environmental gradients, it must be kept in mind that environmental measurements are not always independent of vegetation. For example, Steiger (1930), working on prairies of Eastern Nebraska, found that the clipping of plant tops resulted in an immediate increase in soil temperatures, an increase in evaporation rates and a decrease in soil moistures in the upper soil layers. Thus, it is apparent that the vegetation of a site has a strong influence upon soil moisture, and that all these factors are important in determining the vegetation.

Of the environmental factors measured, soil

TABLE V. Frequency values for all species[1] which occurred in ten or more quadrats. The frequency values were calculated on the basis of the percentage of quadrats of occurrence in each soil-depth group; e.g., *Aster ptarmicoides* occurred in 11% of the 38 quadrats with a soil depth between 0 and 2 inches.

| Soil Depths, inches | 0-2 | 2-4 | 4-8 | 8+ |
|---|---|---|---|---|
| No. of quadrats | 38 | 104 | 28 | 70 |
| SPECIES | | | | |
| Aster ptarmicoides | 11 | 6 | — | — |
| Liatris cylindracea | 55 | 39 | 8 | — |
| Viola pedata | 58 | 21 | 16 | 1 |
| Solidago nemoralis | 32 | 16 | 8 | — |
| Panicum perlongum | 21 | 16 | 11 | — |
| Aster linariifolius | 18 | 18 | 8 | — |
| Antennaria spp. | 18 | 7 | 8 | — |
| Petalostemum purpureum | 3 | 2 | — | — |
| Bouteloua curtipendula | 76 | 65 | 42 | 7 |
| Andropogon scoparius | 82 | 53 | 18 | 12 |
| Aster sericeus | 66 | 41 | 26 | 9 |
| Sporobolus heterolepis | 61 | 31 | 34 | 3 |
| Aster azureus | 76 | 58 | 34 | 27 |
| Carex pensylvanica | 21 | 18 | 3 | 4 |
| Melilotus spp. | 16 | 14 | 8 | 6 |
| Andropogon gerardi | 74 | 71 | 61 | 57 |
| Solidago rigida | 5 | 10 | 5 | — |
| Convolvulus arvensis | 3 | 7 | 5 | 7 |
| Anemone cylindrica | 5 | 6 | 3 | 6 |
| Coreopsis palmata | 24 | 21 | 21 | 24 |
| Solidago speciosa | 16 | 9 | 13 | 10 |
| Potentilla arguta | 11 | 11 | 8 | 12 |
| Physalis heterophylla | 5 | 2 | 8 | 7 |
| Prunus serotina | 10 | 7 | 11 | 6 |
| Kuhnia eupatorioides | 8 | 17 | 18 | 10 |
| Ratibida pinnata | 16 | 18 | 24 | 7 |
| Panicum oligosanthes | 8 | 12 | 18 | 1 |
| Euphorbia corollata | 40 | 53 | 66 | 62 |
| Populus tremuloides | 8 | 11 | 26 | 1 |
| Amorpha canescens | 29 | 42 | 58 | 57 |
| Aster ericoides | 3 | 1 | 8 | 7 |
| Stipa spartea | 11 | 5 | 18 | 1 |
| Poa pratensis | 29 | 54 | 90 | 81 |
| Equisetum kansanum | — | 6 | 26 | 3 |
| Vitis vulpina | 3 | 7 | 8 | 3 |
| Panicum leibergii | — | 11 | 34 | 30 |
| Physalis virginiana | 8 | 13 | 13 | 23 |
| Rosa spp. | 8 | 6 | 18 | 34 |
| Monarda fistulosa | 8 | 17 | 32 | 50 |
| Sorghastrum nutans | 3 | 11 | 32 | 77 |
| Asclepias syriaca | — | 1 | 8 | 14 |
| Desmodium illinoense | — | — | 3 | 15 |

[1] See footnote to Table III.

depth appeared to be the only variable independent of vegetation. The occurrence of thin soils over bedrock on hill crests and of deeper soils in valleys (Fig. 1) has resulted from geological processes of base leveling and is independent, in geological time, of plant activities. Since there is no apparent physiological reason why soil depths should discriminate between plant species, the ultimate causes for the close correlation between soil depths and species composition, as shown in Table V, must be sought in the influence of soil depth upon environmental factors more directly affecting plant growth. There is no apparent way in which soil depth could directly affect surface and sub-surface temperatures since they are the direct result of insolation imposed upon the grassland community from above; variations in these temperatures would appear, therefore, to be more directly related to the shading effect of vegetation (i.e., plant heights as shown in Fig. 5) than to edaphic factors.

TABLE VI. Average values for edaphic factors in the four soil depth classes.

| | SOIL DEPTH CLASSES, INCHES | | | |
|---|---|---|---|---|
| | 0-2 | 2-4 | 4-8 | 8+ |
| Soil Moisture, per cent | 5.5 | 7.9 | 11.5 | 13.4 |
| Soil Temperature, °F | | | | |
| Surface | 111.0 | 103.2 | 92.8 | 89.3 |
| 2″ below surface | 98.4 | 93.4 | 87.5 | 84.7 |
| Water-Retaining Capacities, per cent | 61.4 | 61.2 | 61.1 | 62.8 |

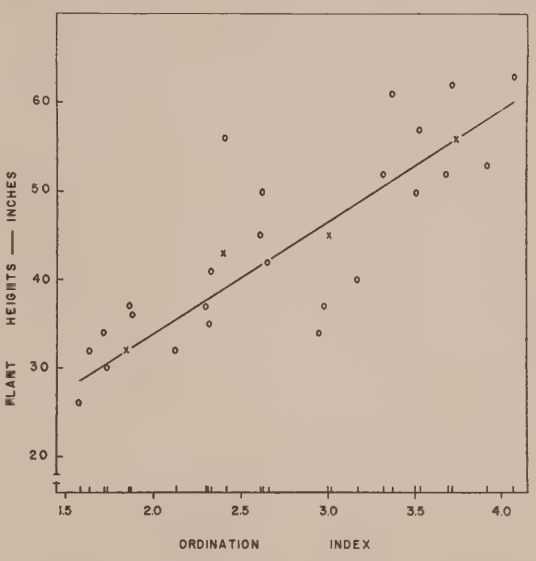


FIG. 5. Plant heights against the plot index ordination. The open circles indicate plot averages for the tallest herbaceous plant in each quadrat while the "x's" denote averages of plots within 1.0 unit intervals.

The influence of soil depths on soil moisture seems a more reasonable explanation. Immediately following a saturating rain, prairie soils are uniformly above field capacity. As gravitational water drains away and with the loss of capillary water directly to the atmosphere and by transpiration, the upper soil layers are dried and water is drawn upward from lower soil depths. On thin soil areas the amount of water available

is relatively small and the supply may soon become exhausted, while in deeper soils capillary water is stored in greater quantity and consequently is available for plant growth over a longer time. This phenomenon is clearly shown in the substantially higher percentages of soil moisture in deep soil areas, as contrasted with thin soil areas, during periods of prolonged drought (Table VI). Thus it appears that, on this prairie, soil depth controls soil moisture, soil moisture directly influences species composition, and species composition influences soil moisture through its influence on surface and sub-surface temperatures. It seems clear therefore, that the primary environmental factor determining the local distribution of plant species there is soil depth.

## Discussion

There is no evidence in this study that the phytosociological behaviors of the species are due simply to the sorting of species along gradients of the physical environment. Although factors of the physical environment do correlate well with vegetational patterns, the biota can and does modify the physical environment (Steiger 1930, Geiger 1957, McIntosh 1957, and others). It should be emphasized, therefore, that factors which restrict one species to thin-soil areas and permit another to reach its greatest importance on deep soils, are, in part, biotic. Competition between species is suggested as the primary, but not the only, biotic agent which determines the local distribution of species. Field work indicates, for example, that when xerophytic species grow in mesic habitats without competition (e.g., in recently disturbed areas) they usually show more vigor than when grown without competition in xeric habitats.

No attempt was made to classify the vegetation in the ordinary sense, but the arrangement of vegetational data along ordination series demonstrated the phytosociological relationships between the species compositions of the plots (Table II and III and Figures 2 and 3) and between individual species (Table V). When the phytosociological behavior patterns of species on this prairie were compared to the behavior of the same species as reported by Curtis (1955), in 157 prairie stands in southern Wisconsin, the behavior patterns in the 2 studies were remarkably similar. *Andropogon scoparius, Bouteloua curtipendula* and *Panicum prelongum,* for example, reached their greatest importance in this study on thin-soil (dry) areas and these species were among those selected by Curtis as indicators of dry prairies. Similarly, *Panicum leibergii* and *Desmodium illinoense* were used by Curtis as indicators of mesic prairie and they are found only on the deeper soil (mesic) areas in this study. Results strongly suggest, therefore, that one of the principal environmental factors influencing the species compositions of the 'mesic-dry" and the "dry" Wisconsin prairies (in the nomenclature of Curtis), is the dominant influence which soil depths exert in controlling soil moistures. Species such as *Andropogon gerardi* which showed a ubiquitous behavior pattern in Curtis' extensive survey showed a similar pattern on this small prairie.

Serious consideration was given to the possibility of applying more elaborate ordination methods (Goodall 1954; Bray and Curtis 1957) to data from the Lodi Prairie, but such an approach was abandoned after preliminary tests indicated that distributions of plant species on this prairie were adequately explained by simpler ordination techniques and when environmental variability on the prairie proved insufficient to justify the additional computational labor necessary to implement more elaborate ordination methods.

Variation in soil depths and consequent variation in soil moisture have been suggested as the principal agents determining the distributions of plant species on this prairie. If so, it is reasonable to suggest that a group of quadrats with similar soil depths from nearby prairies would show similar species compositions. Such data are available from Anderson's (1954) study of the dry-lime prairies of southwestern Wisconsin. Anderson randomly drew 20 "thin-soil" and 20 "deep-soil" (i.e., 4 in. or less; 4 in. or more) 1-$M^2$ quadrats from a number of Wisconsin prairies and grouped them into a "thin-soil prairie" and a "deep-soil prairie." His list of species with distinct preference for shallow soils matches very closely the list found in the upper portion of Table V while those species which showed a preference for deeper soils in his study are found at the bottom of the same list. Anderson also called attention to the similarities in species composition between the thin-soil prairies of Wisconsin and those found in Ohio (Jones 1944) and Eastern South Dakota (Harvey 1908). These similarities add confidence to the conclusion that soil depth is the primary causative agent determining the distribution of species on the Lodi Prairie.

No distinct correlations between plant distribution and the water-retaining capacities of the $A_0$ horizons were apparent on the Lodi Prairie. This contrasts with reports by Partch (1949) and Curtis (1955) for Wisconsin prairies. Absence

of such correlations on the Lodi Prairie was probably due to the dominant role of soil depths in determining soil moistures. The total amount of growth-water retained on a thin-soil area after gravitational water has drained away is comparatively small, and the moisture supply, which cannot be replenished from below because of the impervious bed rock, may soon be exhausted by evaporation and transpiration, and plant growth may then be limited. In contrast, the supply of growth-water in the upper horizons of deeper soil areas, although lost at the same or at a greater rate as on thin soils, is replenished from below and growth-water is available for a comparatively long time. Thus, though a shallow soil may have a high water-retaining capacity, it is not able to maintain a soil-moisture level adequate for the survival of any but xerophytic species during periods of prolonged drought. In deeper soils, the influence of water-retaining capacities is much more pronounced and appears to play an important role in determining the distribution of growth-water.

Internal drainage of prairie soils may also be a significant factor in determining soil moistures, since gravitational water drains from areas of high topographic positions and flows toward areas of lower elevations. This suggests that gravitational water may be present for extended periods at lower elevations and thus may influence plant growth on these sites. It was determined, however, that gravitational water on the Lodi Prairie drains away within 2-4 days after heavy rains and this period seemed too brief to exert a profound influence on the distributional patterns of species.

McIntosh (1957) was unable to find correlation between species distribution and soil depth in a heterogeneous woods in southern Wisconsin. There, light intensity and soil pH were the only environmental factors which showed correlations with the vegetation, and the value levels of these factors in the woods were controlled by the vegetation. Thus, it apeared that the tree canopy controlled soil moistures by regulating the amount of light which reached the forest floor and the influence of soil depths and water-retaining capacities was so modified by light penetration that their correlation with the vegetation was not evident. McIntosh concluded "that distributional patterns of species were determined by variations in the history of local areas within the woods and that phytosociological relationships between species were primarily, but not entirely, successional.

There is no evidence that distributional patterns exhibited by the plant species on the Lodi Prairie are successionally related. According to its present owner, the prairie has been undisturbed and unburned for at least 25 years (probably much longer) and it showed no signs of disturbance or fire. The existence of similar species compositions on similar topographic situations throughout the Middle West (Anderson 1954), would also indicate the comparative stability of species composition on the prairie. It appears that physiographic situations on the Lodi Prairie present environmental conditions which fall within the ecological amplitudes of the available flora and that the physical environment is the principal agent which has discriminated between the species and determined their local distributions. The first sorting of species on this area was therefore determined by the distribution of the various environmental levels; species able to survive within a given set of environmental levels then competed among themselves and, as a result, associated or dissociated with one another. Once the distributional patterns were established, however, there seems little the plants could do by their own actions to bring about any modifications in the patterns. Similar local distribution of grassland plants have been described by Dix (1958) in western North Dakota and by Weaver (1958) in western Iowa.

Evidence does exist, however, that the Lodi Prairie is currently being invaded by woody species. A grove of *Populus tremuloides* was well established near the north end of the prairie at the time of the study and it appeared to be rapidly extending its area of domination across the prairie. Other woody species found scattered through the prairie were *Prunus serotina, Quercus macrocarpa, Juniperus virginiana, Carya ovata, Rubus* sp., and *Vitis vulpina.* While the present species distribution on the Lodi Prairie are primarily dependent on the distribution of environmental factors, especially soil depths, the future species distribution may well depend upon successional relationships. As woody species invade the prairie they will strongly modify light conditions and consequently soil depth will no longer be the principal factor determining plant distributions. If the prairie remains unburned it will undoubtedly give way to forest (Costello 1931, Cottam 1949) while periodic burning would retain it in grassland (Dix and Butler 1954).

Correlations between environmental factors and vegetation do not, of course, prove causal relationships, but circumstantial evidence of consistent and strong correlations aids greatly in the assign-

ment of probable causes to vegetational patterns. The necessity for experimental evidence in obtaining a complete and final insight into the puzzling and multifarious array of factors involved in the environmental complex is apparent. It is equally apparent, however, that a random approach to the study of this complex has proved inefficient. Goodall (1954) has pointed out that "there is much to be said for the view that the complexes of environmental factors determining plant distributions can be indicated and measured better indirectly, through the plants themselves, than by direct physical measurements; . . ." It is suggested, therefore, that for studies on the physical environment to be of maximum value, they should be designed to include consideration of the phytosociological interrelationships between the organisms occupying that habitat. This is no less true for experimental studies on the autecology of plants. It is reasonable to question, for example, whether the individuals of *Andropogon gerardi* which are associated with *Liatris cylindracea, Bouteloua curtipendula* and *Panicum prelongum* on the Lodi Prairie are genetically the same as other individuals of the species which occur with *Sorghastrum nutans* and *Monarda fistulosa,* for the physical and biotic environments in which they grow have been shown in the present study to be significantly different. Thus, if individuals of *Andropogon gerardi* from the Lodi Prairie were to be used in experimental studies, to identify them simply as having been collected "near Lodi, Wisconsin" without designating their phytosociological positions would have the effect of unnecessarily limiting the interpretations which could be rightfully placed upon the experimental data.

## Summary

1. An intensive study was made of the phytosociological and environmental interrelationships of plant species occurring on a small prairie in southcentral Wisconsin. The prairie was surveyed, a grid system established, and the occurrence of species and environmental measurements were recorded in 250 one $m^2$ quadrats; one quadrat was located at each intersection of the grid lines. The environmental factors measured were soil depth, soil moisture, surface and sub-surface temperatures and water-retaining capacity of the $A_0$ soil horizon.

2. The principal plant families contributing to the flora of this prairie were the *Compositae, Gramineae, Leguminosae* and *Asclepiadaceae.* These accounted for 53% of the species on the site. This family composition was shown to be similar to that of other Wisconsin prairies and to grasslands in eastern Nebraska.

3. To reduce the volume of data the prairie was divided into 25 plots; each plot contained 10 quadrats. A coefficient of similarity index was then used to order the plots in a linear fashion. When behavior of individual species was plotted against this ordination, virtually all species showed orderly behavior patterns against the gradient.

4. Correlations between the plot ordinations and various environmental factors suggested that soil depth was the environmental factor which primarily determined the local distribution of plant species on the prairie. It was found that soil moisture was positively correlated with soil depth, that surface and sub-surface temperatures were negatively correlated with soil depth, and that water-retaining capacities were not correlated with any other environmental factor. The influence of soil depth on soil moisture appeared to account, in a large part, for the correlations. All measured environmental factors, with the exception of water-retaining capacity, showed strong correlations with species distributions.

5. The distributional patterns of the species on this prairie do not appear to be successionally related.

6. The behavior of the species along environmental gradients agreed well with the behavior of the same species along similar gradients as demonstrated in several extensive studies of Wisconsin prairies. It was suggested that soil drought, as reflected in soil moisture and controlled by soil depth, is the principal environmental factor which determines the species composition of the "mesic-dry" and "dry" prairies of Wisconsin.

## Acknowledgments

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# WINTER DEER ACTIVITY IN THE WHITE CEDAR SWAMPS OF NORTHERN WISCONSIN[1]

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Lowland swamp communities, particularly those dominated by white cedar (*Thuja occidentalis*) provide the major portion of the winter range of the white-tailed deer (*Odocoileus virginianus*) in northern Wisconsin (Christensen 1954). A review of the history of the winter deer range in northern Wisconsin revealed that lowland white cedar swamps have been used for winter range from the earliest times for which historical records are available (Christensen 1954, 1959). The cutting of the mature forests in northern Wisconsin at the time of extensive settlement (about 1850) resulted in a great increase in the number of deer because of the increase in the amount of summer deer range (Swift 1946). The intensity of utilization of white cedar swamps by wintering deer increased greatly as the total number of deer increased. Today there are large numbers of deer in northern Wisconsin and the amount of winter range available to them has steadily declined due to concurrent cutting and draining of white cedar swamps.

Observations of the winter deer range in northern Wisconsin (Keener 1952, Swift 1948, Smith 1955) indicate that high deer populations have caused serious damage to the white cedar swamps used as deer yards. Such range damage is frequently assessed on the basis of the relative abundance and condition of the food species in a particular deer yard (Passmore and Hepburn 1955; Davenport *et al.* 1953). Another type of deer range deterioration which has not as yet been reported upon in the northern Lakes States region is the influence of winter deer activity on the physical environment of white cedar swamps. At the initiation of the present study, it was believed that a three-month confinement each year of a high number of deer would result in significant alterations in the soil as well as the bontanical features of the white cedar swamps. Attention, therefore, was directed to the effects on the soil environment, and in particular to the correlation of such effects with the effects upon the botanical

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composition previously studied by Cottam and Curtis (1956). It was hoped that a study with this approach would help in understanding how winter disturbance by deer influences not only the individual plant species but the over-all stability of the cedar swamp communities in northern Wisconsin.

The field data were collected during the summers of 1956 and 1957. The author wishes to acknowledge the aid of Drs. J. T. Curtis and G. Cottam, University of Wisconsin, in this study. The nomenclature for plant species follows Gleason (1952).

## Objectively Measuring Winter Deer Activity

An objective method for measurement of deer activity was developed by Cottam and Curtis (1956), who followed a procedure similar to those for measuring the intensity of grazing pressure by cattle on grassland and pasture areas (Dyksterhuis 1949, Cawley 1958, Dix 1959). The initial step was the comparison of two similar groups of lowland forest communities existing in northern Wisconsin—those which have been disturbed by winter deer activity (Christensen 1954) compared to those which have not experienced any great degree of winter deer activity (Jones 1955). For comparing the botanical composition of these two groups of lowland communities (which will be referred to as deer yards and non-deer yards), the stands in each group were arranged into phytosociological ordinations, based on tree composition (Greig-Smith 1957, Phillips 1959). It was observed by Cottam and Curtis that the resulting phytosociological ordinations were very similar. This suggested to them that differences which might exist in the phytosociological behavior of the understory species in deer yards and non-deer yards could be attributed, at least indirectly, to winter deer activity, and not to differences in environmental factors controlled by tree composition. It seems that the period of severe deer disturbance in northern Wisconsin cedar swamps is relatively recent compared to the ages of the trees.

Cottam and Curtis reported that some shrub and herb species appear to be uninfluenced by winter deer activity, that is, they are equally common in deer yards as in non-deer yards. Other species, however, exhibit a definite differential response to deer activity. Some species seem to find the influence of winter deer activity beneficial in some way and are thus found more commonly in deer yards than non-deer yards. Other species seem to be intolerant of deer disturbance, and such species are found less often or are completely absent in deer yards. Those species which tend to become more common under deer activity are called "increasers", and those which tend to become less common are called "decreasers".

Cottam and Curtis made use of the differential response of the increaser and decreaser species in their method. A total of forty understory species were selected which possess value as indicators of deer activity in cedar swamps, *viz.*, ten extreme decreasers, which disappear or are reduced markedly in deer yards: *Chelone glabra, Clemantis virginiana, Cypripedium Calceolus, Habenaria obtusata, Moneses uniflora, Menyanthes trifoliata, Solanum nigrum, Smilacina racemosa, Smilacina trifolia* and *Symplocarpus foetidus;* ten moderate decreasers, which are less sensitive to deer activity, but show a tendency to decrease in deer yards: *Botrychium virginianum, Caltha palustris, Cornus rugosa, Eupatorium perfoliatum, Glyceria striata, Mitella diphylla, Rhus radicans, Ribes triste, Scutellaria galericulata* and *Taxus canadensis;* ten moderate increases, which can tolerate deer activity and in some degree are benefited by disturbance: *Athyrium Filix-femina, Calamagrostis canadensis, Cornus alternifolia, Fragaria virginiana, Ilex verticillata, Nemopanthus mucronatus, Pteridium aquilinum, Ribes lacustre, Rubus*-raspberry and *Scutellaria laterifolia;* and ten extreme increasers, which are found in considerably greater numbers in deer yards: *Aster umbellatus, Brachyelytrum erectum, Bromus purgans, Corylus cornuta, Lycopodium clavatum, Lycopodium obscurum, Oryzopsis asperifolia, Matteuccia Struthiopteria, Rhus typhina* and *Schizachne purpurascens.*

To calculate a numerical index value for any given lowland swamp, the number of extreme decreaser indicator species which are present is weighted (multiplied) by 1, the number of moderate decreasers is weighted by 2, the moderate increasers by 3 and the extreme increasers by 4. The sum total of weighted values is then divided by the total number of indicator species present. For example, a given white cedar deer yard might have no extreme decreasers, 2 moderate decreasers, 5 moderate increasers and 7 extreme increasers. The calculation is as follows:

$$\frac{(0 \times 1) + (2 \times 2) + (5 \times 3) + (7 \times 4)}{0 + 2 + 5 + 7}$$

$$= \frac{47}{14} = 3.36 \times 100 = 336$$

This index value, called the Deer Activity Index (D.A.I.) value, can theoretically vary from 100 for wholly protected areas to 400 for the most

severely utilized deer yards. The actual range of values for 98 lowland communities classified by Cottam and Curtis was from 125 to 380. All of the communities studied by Jones (1955) have D.A.I. values at or below the midpoint of the scale; all but a few of the areas studied by Christensen (1954) have D.A.I. values above 250. As a result of these findings, it was concluded by Cottam and Curtis that the D.A.I. method provides an accurate and objective method for measuring the intensity of winter deer activity. The 98 communities classified formed a smooth gradient separating deer yards and non-deer yards. To facilitate discussion, however, the areas with D.A.I. values below 250 are called non-deer yards, and those with values above 250, deer yards.

Included as a part of the field studies conducted by the writer was a cross check of the D.A.I. values. Thirty-seven lowland cedar communities (Fig. 1), representative of the entire D.A.I.

FIG. 1. Distribution of the 37 white cedar swamps studied in northern Wisconsin.

gradient and which had been studied previously by Christensen or Jones, were revisited and data were collected so that a D.A.I. value could be calculated for each stand. A comparison of the D.A.I. values of each of the 37 stands with the earlier D.A.I. values calculated by Cottam and Curtis, revealed that 26 (70%) of the areas had D.A.I. values within 20 units (plus and minus) of the first D.A.I. values. This indicates that rather close duplication of D.A.I. values is possible when the field data are collected by different workers. The fact that the field data were collected several years apart in probably responsible for the index values not showing an even closer agreement. As 78% of the areas revisited had index values to some degree *higher* than the first index value, it is very probable that there has been a change in the botanical composition since the areas were first studied, presumably as a result of continued deer disturbance.

## EFFECTS OF DEER ACTIVITY ON CEDAR SWAMP VEGETATION

In delineating the understory species exhibiting differential response to winter deer activity, Cottam and Curtis (1956) discovered that many understory species which tend to become more common in cedar swamps under deer disturbance (the increasers), show a shift, to the left, of the peaks of their amplitude of tolerance curves along the northern lowland continuum gradient (Christensen *et al.*, 1959). Among the species showing a shift, the optimum conditions for growth in lowland communities not used as deer yards are found in stands more mesic than white cedar swamps, that is, in stands dominated by black ash (*Fraxinus nigra*), yellow birch (*Betula lutea*), and red maple (*Acer rubrum*). Among the lowland swamps used as deer yards, these dominated by white cedar. The exact nature of shifting species reach their optimum in stands these shifts is revealed by Fig. 2, where the percentage presence of these species in deer yards and non-deer yards is plotted along the northern lowland continuum gradient (Christensen *et al.* 1959). The continuum gradient has been partitioned into equal segments to facilitate the presentation. A rather high percentage of the total understory species show similar shifting behavior. Of the 166 plants which have a percentage presence of at least 10% in any of the lowland continuum segments, 77 (46%) exhibit a shift. It is apparent that lowland white cedar swamps subjected to winter deer activity are being encroached upon by a more mesic understory flora; this is currently taking place without a significant change in the tree composition.

Quantitative data collected on the woody food species (Christensen 1954; Habeck 1959a) generally support the information gathered by more subjective field methods. As the intensity of deer disturbance increases, the amount of available browse decreases. White cedar, which is a highly preferred winter food, is heavily utilized in stands which have low D.A.I. values. Two maple species (*Acer rubrum* and *A. spicatum*) are also heavily consumed as deer foods, but these species have an ability to resprout vigorously fol-

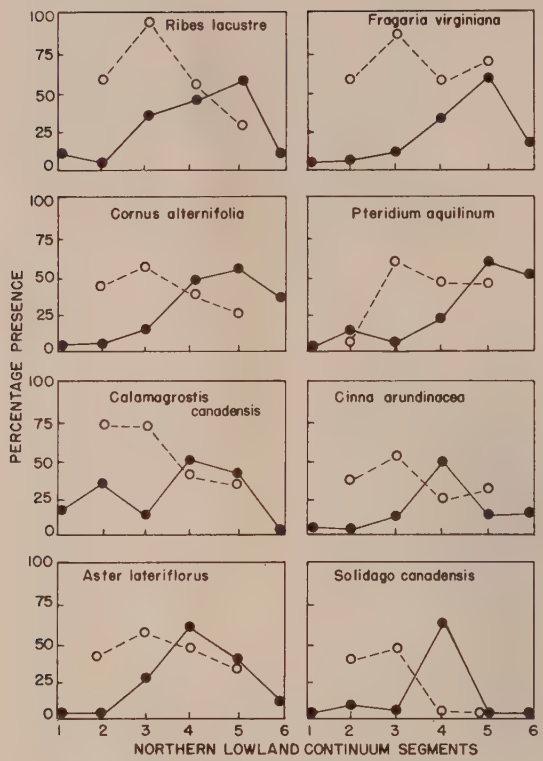


FIG. 2. Illustration of the shift, to the left, of the peaks of the amplitude of tolerance curves for 8 understory species. The ordinate values are percent presence. The non-deer yard values (solid lines) have been calculated for each of six 165-unit segments within a northern lowland continuum range of C.I. 1000 to C.I. 1990. The deer yard values (dashed lines) have been calculated only for a lowland continuum range of C.I. 1165 to C.I. 1725, represented by segments 2, 3, 4, and 5 in these graphs.

lowing moderate browsing and quantitative data for these maple species indicate that they can maintain themselves under deer activity. Balsam fir (*Abies balsamea*) also becomes more abundant in white cedar swamps used as deer yards; this species provides a very poor quality winter food and it is believed that the removal of other tree reproduction by deer browsing has allowed balsam fir reproduction to increase.

## Effects of Deer Activity on the Physical Environment of Cedar Swamps

It was hoped that a study of the influence of winter deer activity on the physical environment of cedar swamps, particularly the soil features, would aid in understanding the differential responses of the understory species described earlier and also, to reveal some information on the over-all lowland community stability under the impact of deer disturbance. The areas in which soil features were studied are the same as those shown in Fig. 1. The soil features studied and the field methods used in collecting the data are described below.

### *Methods*

*Soil Compaction*—Data were collected at each of 10 sampling points which were spaced approximately 120 feet apart along a predetermined compass line. A measure of soil compaction was gained by measuring soil air permeability. The area around each sampling point was divided into quarters and a reading was taken in each quarter. A sphygmomanometer (Wilde and Voigt 1955) was used in measuring the soil air permeability. The apparatus consists of a steel tube, 15 cm long, a constant pressure rubber chamber and an aneroid manometer, all connected by rubber tubing. The steel tube was placed in the soil and the rubber chamber was inflated with air until a reading of 200 mm. pressure was registered on the manometer. The air in the chamber was then allowed to pass through the steel tube for 10 seconds. The pressure reading on the manometer at the end of this period was recorded. The tabulation of 4 soil air permeability readings at each of 10 sampling points resulted in a total of 40 ten-second readings for each stand. The total was used directly as an index of soil air permeability and soil compaction in a given stand. The instrument used in this study would record a total of 1840 mm of pressure at 40 points if no resistance was placed in the tube, i.e., the pressure would drop from 200 mm to 46 mm in ten seconds if the tube was held in the air. The best aerated soils would thus have total readings somewhat greater than 1840 mm.

*Measure of Peat Decomposition*—The soil in lowland white cedar swamps in northern Wisconsin is largely composed of organic peat of moss and wood origin. A study of the physical composition of peat deposits in non-deer yard swamps (Jones 1955, 1957) has indicated that approximately 50% (by dry weight) of the peat is composed of coarse particles (particles which will not pass through a 5 mm sieve). Although a stabilized water table often permits the perpetuation of lowland white cedar swamps in northern Wisconsin (Christensen *et al.* 1959), whenever there is a change in the moisture conditions leading to more mesic conditions, the white cedar is replaced by more mesic hardwood species. Accompanying such a change in community composition is the increased reduction or decomposition of the peat particles. Under such conditions the percentage of coarse peat particles gradually becomes smaller. An analysis of the peat deposits in the 37 white

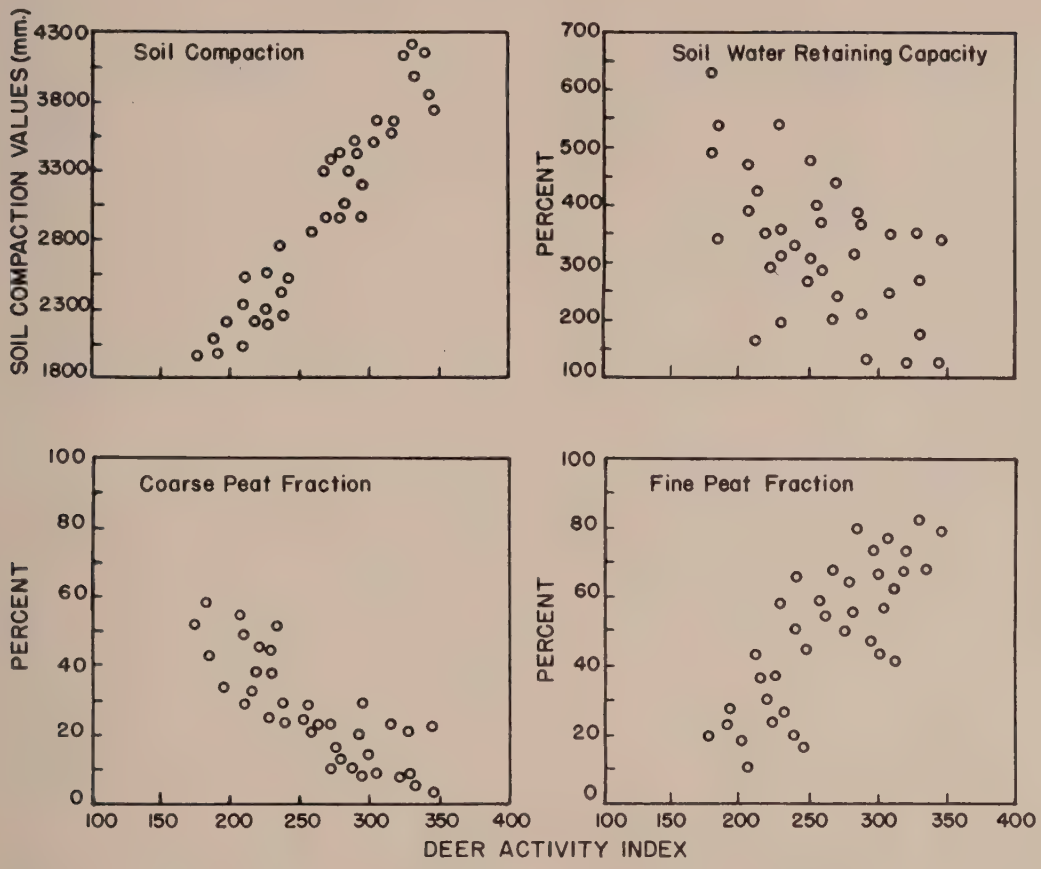


FIG. 3. Correlation of cedar swamp soil data and the Deer Activity Index gradient. Each circle represents the data from one stand. The soil compaction values are totals for forty 10-second readings in each stand. The percentages for soil water retaining capacity are based on dry weight.

cedar swamps provided the opportunity to determine the effects of winter deer activity on the rate of peat decomposition. The methods used in this analysis are described by Jones (1957).

*Soil Water Retaining Capacity*—A soil sample was collected in each of the 37 stands studied. This sample was used in determining the soil water retaining capacity for each stand. The method used in this operation follows that described by Curtis (1956). The values were calculated as percentages of dry weight.

## RESULTS

The data collected on the various soil features were plotted along the D.A.I. gradient. The placement of the data for each stand was based on the D.A.I. value calculated from the field data collected by the writer. The range of D.A.I. for the 37 stands was from 191 to 349, which represented a wide range of winter deer activity. The data for soil compaction (soil air permeability), peat decomposition and soil water retaining capacity are shown in Fig. 3.

There is a remarkably close correlation between soil compaction and the intensity of winter deer activity. A statistical analysis of these data resulted in a correlation coefficient of 0.92. The peat decomposition data also showed a good correlation with deer activity. As the intensity of deer disturbance increases, the percentage of fine peat particles (those which will pass through a 1 mm sieve) increases, whereas the percentage of coarse peat particles decreases. The soil water retaining capacity decreases with increased winter deer activity, from an average of about 520% in lightly used and unused cedar swamps to about 350% in heavily used deer yards.

## DISCUSSION AND CONCLUSIONS

The data on the soil features indicate that winter deer activity has a marked influence on the physical properties of the white cedar swamp soils

in northern Wisconsin. Although there are other soil features which are probably changed under deer activity, the results of this study clearly indicate the direction and magnitude of the changes taking place under the impact of winter deer disturbance.

Soil compaction, peat decomposition and soil water retaining capacity are too closely related to discuss separately. The increased soil compaction and decreased soil air permeability are probably a result of the increase in the percentage of fine peat particles. The actual decomposition of the peat deposits in deer yards may be a direct result of the physical action of the deer when they are confined to the deer yards three months of each year. Although the hooves of the deer are not large, they are very sharp and the soil may be severely altered by the trampling action. The decrease in soil water retaining capacity under deer activity is probably also related to the decomposition of the peat deposits. As the percentage of the fine peat particles increases the ability of a given volume of organic soil to retain water lessens considerably.

On the whole, these soil data support the idea that the white cedar swamps in northern Wisconsin, which are subjected to deer activity, are tending to become more mesic. Many of the changes in the soil features described here would be expected to occur whenever the white cedar community is replaced by a more mesic hardwood forest. The change in presence values of a great many understory species in deer yard swamps may be interpreted as a response to the changes in the physical features of the soil. The understory species which show a shift to the left, as described earlier, have not changed their amplitude of environmental tolerance, but rather, have responded to the more mesic conditions found in heavily used white cedar deer yards. The high percentage of understory species involved in this shift increases considerably the importance of winter deer activity on the over-all community stability. Such changes in the understory may foreshadow more conspicious changes which may occur in the tree composition with continued winter deer disturbance.

The present changes in the understory vegetation and the probable future changes in the tree composition are difficult to evaluate fully at this time. In recent years the deer herd in the central Wisconsin sand plain area has greatly increased, but a quantitative study (Habeck 1959b) has shown that deer disturbance has not harmed the winter range, but has actually increased the available food supplies. The deer in northern Wisconsin, however, experience more severe winter weather, and select white cedar swamps for the protective cover, therefore any disturbance by either man or deer which would lead to a replacement of the white cedar swamps by other non-coniferous communities can not be considered beneficial.

## Summary

The influence of white-tailed deer on the physical environment and vegetation of their winter range was studied in northern Wisconsin. A description of the development and use of an objective method for measuring the intensity of winter deer activity in white cedar swamps is presented. This method, called the Deer Activity Index, was used in ordering the data collected on the vegetation and physical features of the soils of cedar swamps. Winter deer disturbance significantly affected the soils in cedar swamp deer yards. These changes in soil seem to be closely related to changes taking place in the understory vegetation. The study indicates that winter deer activity is influencing markedly the over-all stability of white cedar swamps in northern Wisconsin. The result of severe and prolonged winter deer disturbance in white cedar swamps seems to be the replacement of the cedar swamps by a more mesic vegetation.

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# QUANTITATIVE SEASONAL CHANGES IN THE PHYTOPLANKTON COMMUNITIES OF PYMATUNING RESERVOIR[1,2]

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A study was made of seasonal variations in the plankton communities of a portion of Pymatuning Reservoir over a fourteen month period extending from July, 1955, to August, 1956. This reservoir, located in northwestern Pennsylvania, is being investigated in respect to factors which influence the size and species-composition of algal communities. The work of Tryon and Jackson (1952) showed this to be a highly productive body of water consisting essentially of three ecologically distinct lakes. Sanctuary Lake, the uppermost and most productive of the three portions of the reservoir, was selected for this study. This is an interesting body of water, not only because of its high productivity, but also because of the differences in the nature of its influent waters.

Two distinct drainage areas supply water to the lake (Fig. 1). The eastern portion of the lake receives water from an extensive swamp area extending several miles to the east and south. Linesville Creek drains agricultural and wooded areas and enters the lake from the north. Although only five miles in length, this stream carries considerable silt and organic material into the reservoir. Raw sewage from the town of Linesville (population 1246) is discharged into the stream about one half mile above its mouth. The swamp drainage, while carrying little or no silt and no sewage pollution, contributes the decomposition products of decaying swamp vegetation. No flow measurements are available for either drainage area, so the relative quantities of water from these two sources have not been determined. Orr (1954) compared populations of protozoans from these two drainage areas. Although he included

FIG. 1. Map of the Sanctuary Lake portion of Pymatuning Reservoir showing the locations of 5 sampling stations.

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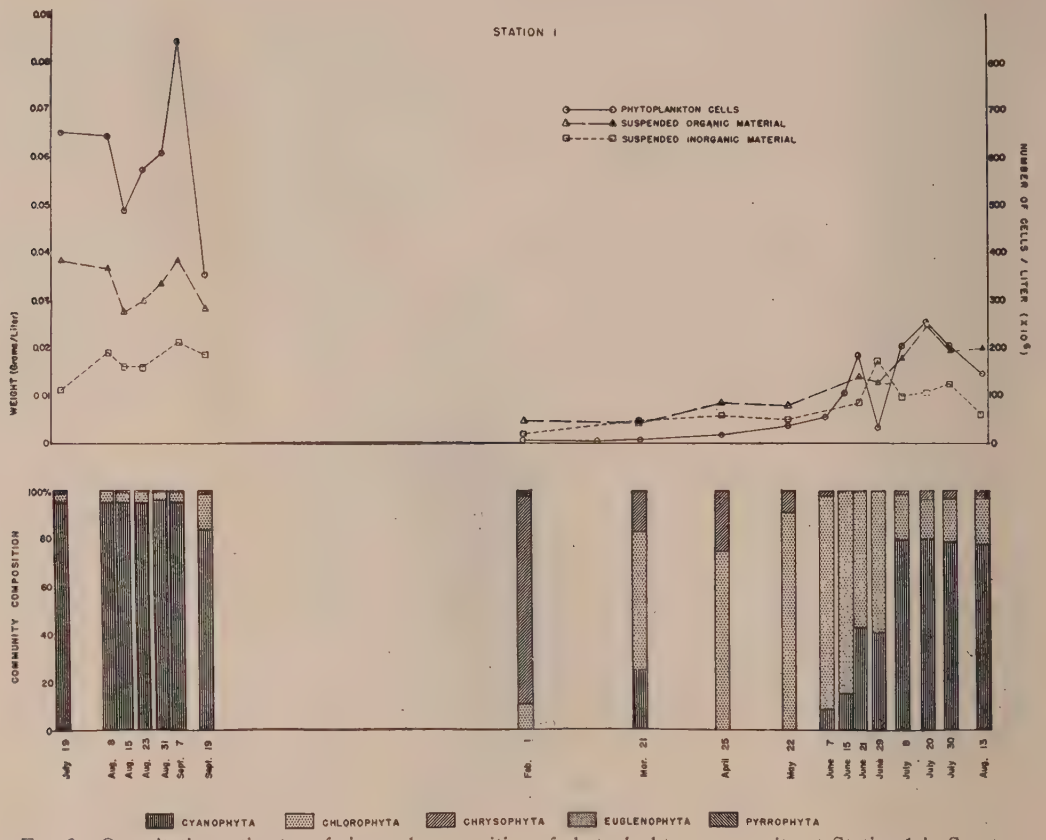


FIG. 2. Quantitative estimates of size and composition of phytoplankton community at Station 1 in Sanctuary Lake for July 19, 1955 to August 13, 1956.

some members of the algal division Pyrrophyta, Euglenophyta, and Chlorophyta in his study, no attention was given to the remaining phytoplankton community.

This investigation was undertaken because no study had been made of the yearly phytoplankton cycle in Pymatuning Reservoir and because no attention had been given to detailed analysis of community structure. Although the quantitative data in this paper deal with conditions in the reservoir during 1955-1956, observations extending over a five-year period have been drawn on to support descriptions of community structure and seasonal changes.

## METHODS

Five collecting stations were established in order to sample outlets of the two main drainage areas and three open water areas. Fig. 1 shows the location of these sampling stations. Station 1 was located at the outlet of a five-mile swamp area; Station 2 was an open-water station in the southern part of the lake; Station 3 was located near the dam and spillway at the outlet of the lake; Station 4 was located near the mouth of Linesville Creek; and Station 5 was in open water in the northern arm of the lake.

Samples were collected from these stations at weekly intervals during summer months, and at bi-weekly or monthly intervals during fall, winter, and early spring. Because of local restrictions during water-fowl hunting season, it was not possible to collect from Stations 1 and 2 during the months of October or November. All samples were taken at a uniform depth of 18 inches and during the winter months were made through the ice cover with a Foerst-Demmerer water sampler.

Cell counts of algae present in each sample were made with a Sedgwick-Rafter counting chamber and a Whipple ocular. In the counting procedure a separate tally was kept for each species. This permitted an analysis of community structure for each station at each sampling date. Whenever possible, algal counts were made directly on unconcentrated samples of lake water.

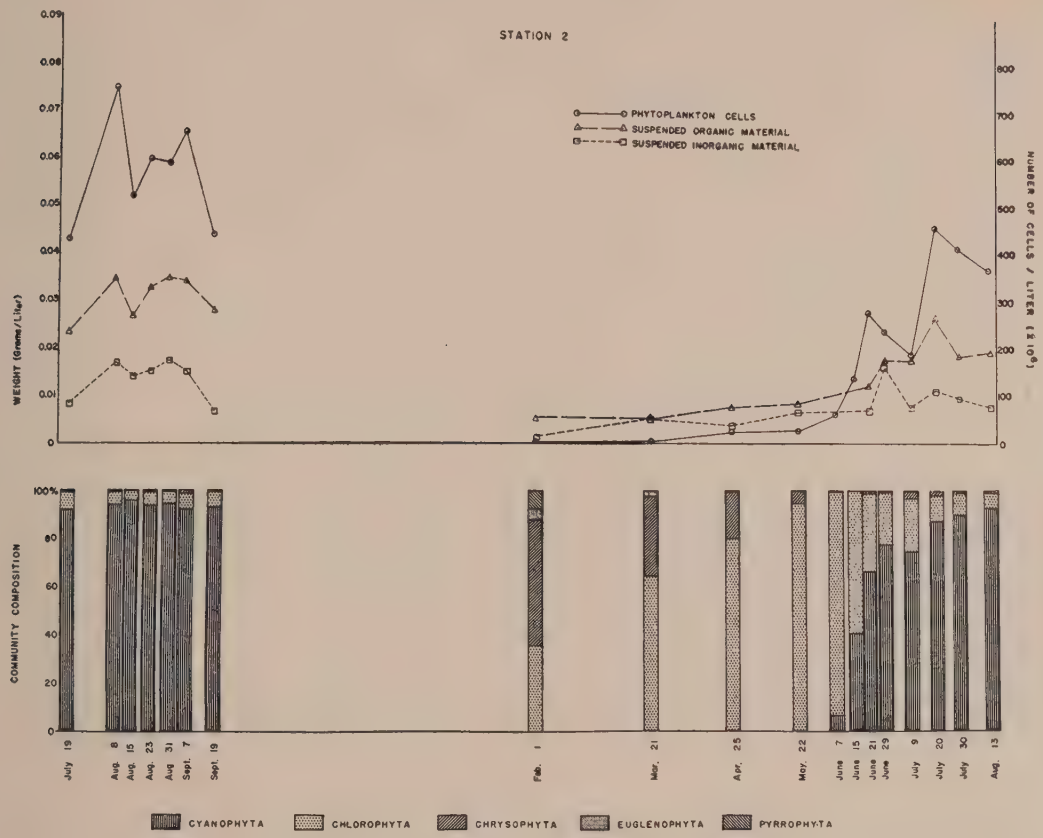


FIG. 3. Quantitative estimates of size and composition of phytoplankton community at Station 2 in Sanctuary Lake for July 19, 1955 to August 13, 1956.

Concentration was necessary for samples taken during winter months. This was accomplished by centrifugation in a Foerst plankton centrifuge. Centrifuged samples were diluted to a suitable volume, usually 100 or 200 ml, in a volumetric flask for counting. For colonial forms, cell numbers were calculated by multiplying colony counts by appropriate factors, arrived at by averaging cell counts made on a large number of typical colonies (Table I).

TABLE I. Factors used in calculation of cell counts for colonial algae.

| | |
|---|---|
| Anabaena | 23 cells/filament |
| Aphanizomenon | 28 cells/filament |
| Aphanizomenon | 280 cells/bundle |
| Coelastrum | 64 cells/colony |
| Coelosphaerium | 250 cells/colony |
| Microcystis | 140 cells/colony |
| Melosira | 9 cells/filament |
| Merismopedia | 32 cells/colony |

Quantities of suspended material in the lake were determined gravimetrically, in triplicate, by centrifuging a liter of water in a Foerst centrifuge, drying the residue in a silicon crucible, and ashing in a muffle furnace. This method permitted calculation of total, organic, and ash weights for each sample. Hartman (1958) has shown that the standard procedure employing a single six to eight-minute run through the centrifuge is not sufficient for removal of suspended materials from the water of Sanctuary Lake. All samples were centrifuged 3 consecutive times.

## RESULTS

Results from cell counts and gravimetric determinations of samples from 5 collecting stations, together with percentage composition of the various phytoplankton communities, are presented in Figures 2 to 6. Although some variation can be seen among cell counts from various stations, there was general agreement in total population size and in community composition among the stations for most of the year. It can be seen further that there was a general, although not always exact, agreement between results for quantities of suspended organic materials ob-

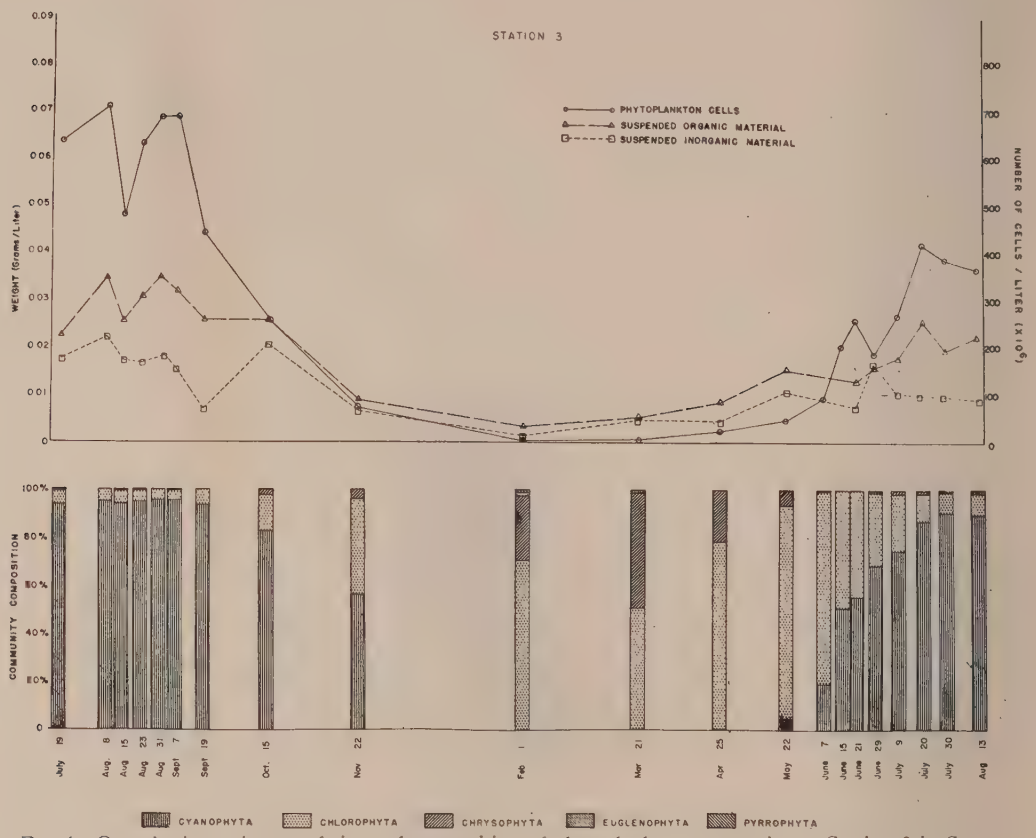


FIG. 4. Quantitative estimates of size and composition of phytoplankton community at Station 3 in Sanctuary Lake for July 19, 1955 to August 13, 1956.

tained by gravimetric procedures and those values obtained by cell counts. Of course, no equivalent comparison can be drawn between results from these two methods but the patterns of increase and decrease are comparable.

Gravimetric values for suspended organic material ranged from a high of 38.2 mg per liter at Station 1 on June 20, 1955 and September 8, 1955 to a low of 3.6 mg per liter at Station 3 on February 1, 1956. Tryon and Jackson (1952) reported a high value of 26.9 mg per liter for samples concentrated by a single-run centrifugation during the summer of 1949. The higher values reported here result in part from the triple centrifugation procedures. Values for suspended inorganic material ranged from 77.1 mg per liter at Station 4 on July 9, 1956 to 1.3 mg per liter at Station 3 on February 2, 1956.

Variation in suspended substances from place to place within the reservoir can be seen in a comparison of the gravimetric results from the 5 stations. Values for suspended inorganic materials at Stations 4 and 5 averaged 2 to 3 times greater than values from the other stations, consistently exceeding the values for suspended organic substances in the northern arm of the lake. This is obviously the result of silt being carried into the reservoir by Linesville Creek. It was apparent throughout this investigation that wind velocity was important in influencing amounts of suspended materials in this shallow body of water. Results from studies now in progress indicate that whereas wind greatly affects suspended inorganic substances, little influence can be noted on amounts of suspended organic materials when measured at regular intervals over a period of several days.

Percentage values shown in the bar graphs of Figures 2 to 6 are calculated from cell counts of individual species grouped by taxonomic divisions and expressed as percentages of total cell counts for each collection. These results indicate the occurrence of summer communities dominated by blue-green species, spring and fall communities dominated by green species and winter communities with greens and diatoms as co-dominants.

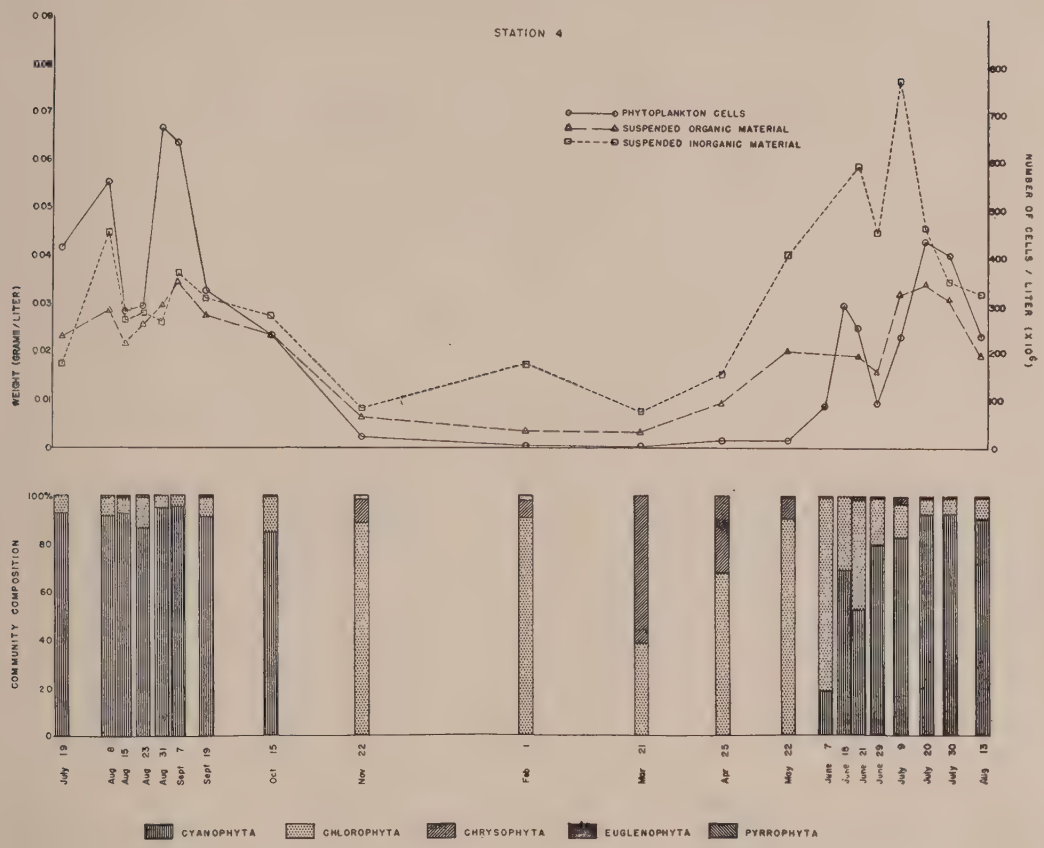


FIG. 5. Quantitative estimates of size and composition of phytoplankton community at Station 4 in Sanctuary Lake for July 19, 1955 to August 13, 1956.

While such percentage values give a panoramic view of seasonal changes in the reservoir, they furnish no information concerning the particular species which comprise the communities. This is obtained only by examining the records of individual stations and correlating them with seasonal changes. Such observations can be less confusing if generalizations are drawn for the lake as a whole rather than for individual collecting stations although it appears to be of value to note major variations from the more typical conditions.

### *Early Summer Community*

Although blue-green species make up the bulk of the summer phytoplankton in Pymatuning Reservoir from June through September, an early summer community can be distinguished on the basis of species composition. These species are normally dominant from early June through the first week in July. Although not observed during 1956, some of these organisms sometimes appear again in large numbers during late August and early September. Species dominant in the early summer community are: *Aphanizomenon flos-aquae* (L.) Ralfs.; *Anabaena circinalis* Rabenhorst; *Anabaena spiroides* var. *crassa* Lemmermann; and *Microcystis aeruginosa* Kuetz., *emend.* Elenkin. Some species typical of the spring community remain as part of the early summer community. Among these are species of the genera *Pediastrum, Scenedesmus, Oocystis, Coelastrum,* and *Sphaerocystis.*

### *Mid-Summer Community*

This algal community, consisting primarily of blue-green species, dominates the reservoir from early July through September. Its members reach extremely high concentrations during early August. The dominant species throughout this period is *Microcystis aeruginosa* Kuetz. *emend.* Elenkin. Other species associated with this dominant form during this period are: *Microcystis incerta* Lemmermann, *Coelosphaerium Naegelianum* Unger; *Aphanocapsa pulchra* (Keutz.) Rabenhorst; *Anabaena spiroides* var. *crassa* Lemmermann; *Gom-*

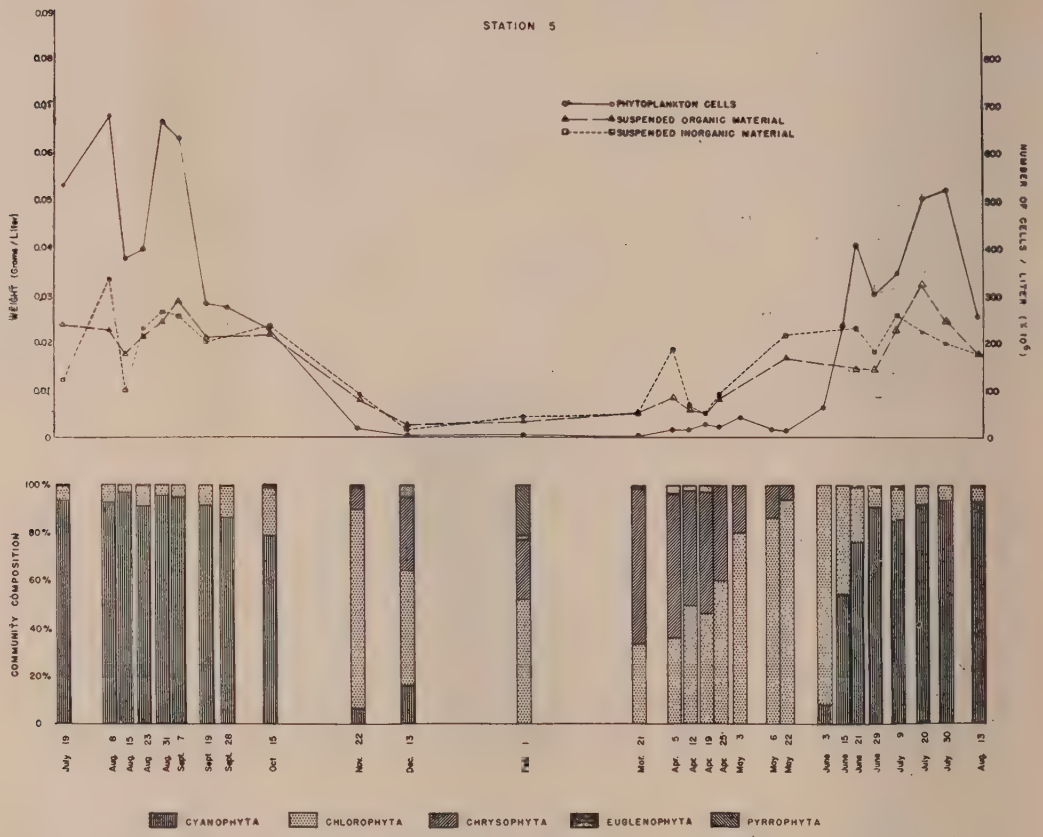


FIG. 6. Quantitative estimates of size and composition of phytoplankton community at Station 5 in Sanctuary Lake for July 19, 1955 to August 13, 1956.

*phosphaeria aponina* Kuetz.; *Pediastrum Boryanum* (Turp.) Meneghini; and *Scenedesmus quadricauda* (Turp.) Brébisson.

### *Fall Community*

The period extending from early September until mid-November is characterized by a gradual decrease in the summer blue-green population, a rise and subsequent fall in numbers of green algae, and finally an increase in diatoms as the winter season approaches. This fall pulse of green algae has as its typical members: *Scenedesmus quadricauda* (Turp.) Brébisson; *Pediastrum Boryanum* (Turp.) Meneghini; *Planktosphaeria gelatinosa* G. M. Smith; *Crucigenia quadrata* Morren; and *Actinastrum Hantzschii* Lagerheim. Several species of *Stephanodiscus, Melosira, Synedra,* and *Asterionella* appear in moderate numbers during this season.

### *Winter Community*

Extending, in general, from mid-November through April the winter phytoplankton community is dominated by diatoms and several species of green algae. Species typical of this winter community are: *Stephanodiscus astraea* (Ehr.) Grunow; *Melosira ambigua* (Grun.) O. Mull.; *Melosira granulata* (Ehr.) Ralfs.; *Synedra acus* var. *angustissima* Grun.; *Asterionella formosa* Hassall; *Nitzchia acicularis* W .Smith; *Stephanodicus niagarae* Ehrenberg; *Fragilaria capucina* Desmaziéres; *Navicula pupula* Kuetzing; *Pediastrum Boryanum* (Turpin) Meneghini; *Scenedesmus quadricauda* (Turpin) Brébisson; *Schroederia setigera* (Schroed.) Lemmermann; *Tetrastrum staurogeniaeforme* (Schroed.) Lemmermann; *Chlamydomonas* sp.; and *Dinobryon sertularia* Ehrenberg. The latter two genera were most common at Stations 1 and 2, the area most influenced by drainage from the swamp. The presence of these organisms and of rather large numbers of *Peridinium* sp. at Station 5 in the February collection, represents the greatest departure from a uniform composition for the reservoir shown in the entire study. This is perhaps to be expected since, as a result of the ice cover, there

is less opportunity for mixing of the water during the winter period.

*Spring Community*

The transition from the winter community to a spring community is characterized by the appearance in late March, among the predominately diatom community, of such forms as *Schroederia Judayi* G. M. Smith and *Tetrastrum staurogeniaeforme* (Schroed.) Lemmermann. The true spring phytoplankton community of Pymatuning Reservoir is characterized by an abundance of unicellular and colonial green algae. During the period of study dominance of this community was of relatively short duration, extending from mid-May into early June. The number of species comprising this community was quite large and included the following: *Pediastrum Boryanum* (Turp.) Meneghini; *P. duplex* var. *gracillimum* West and West; *Scenedesmus quadricauda* (Turp.) Brébisson; *Oocystis Borgei* Snow; *O. elliptica* W. West; *O. pusilla* Hansgirg; *Tetrastrum staurogeniaeforme* (Schroeder) Lemmermann; *Coelastrum microporum* Naegeli; *Crucigenia quadrata* Morren; *Sphaerocystis Schroeteri* Chodat; *Planktosphaeria gelatinosa* G. M. Smith; *Crucigenia fenestrata* Schmidle; *Trachelomonas* sp.; *Lagerheimia subsalsa* Lemmermann; *Cosmarium* sp.; *Gloeocystis gigas* (Kuetzing) Lagerheim; *Staurastrum* spp.; *Chroococcus limneticus* Lemmermann; and *Pandorina morum* (Muell.) Bory.

As noted above, certain of these species persist into the early summer community, although they were not dominant members of that community.

## Discussion

Since its completion and initial filling in 1934, Pymatuning Reservoir has been recognized as a highly productive aquatic area. Extensive deposits of organic muck, which accumulated when the area was a vast bog and swamp forest, were inundated in its construction and undoubtedly play an important role in the eutrophic nature of its waters. Even though large amounts of this organic bottom material have been suspended and washed out of the reservoir, particularly during the early years of its existence, deep deposits still remain. The heavy silt content of the water in the areas of Stations 4 and 5 substantiate the observation that silting is rapidly occurring in the north end of Sanctuary Lake. What influence this will have on the over-all productivity of the reservoir will be interesting to follow.

It is of course true that the eutrophic condition of the reservoir is aided by the organic pollution from Linesville Creek and by dissolved and suspended materials entering from the remaining swamp area. No quantitative estimates on the organic materials from either source have been made to date although it appears that a greater amount of material is contributed by Linesville Creek. The silt from this stream could have a detrimental effect on the development of phytoplankton in the immediate area (Ellis 1936), although this is not indicated by results from the present study. The presence of suspended silt also affects light penetration. Using data furnished from Sanctuary Lake, Verduin (1954) calculated that the average effectiveness of light quenching by suspended materials in this lake was 30 per cent higher than values for the water of the Bass Island region of Lake Erie and about 50 per cent higher than values reported for West Lost Lake, Michigan.

Because of the large number of different methods used in counting populations of phytoplankton, and the possibilities of differences in interpretation and execution of any one procedure, it is always difficult to draw accurate quantitative comparisons between the results of different workers. Furthermore the use here of triple centrifugation for obtaining gravimetric results, while obviously producing values of greater reliability, makes even these values difficult to compare with those of other workers. Rawson (1956) has discussed the problems of characterizing plankton populations and particularly the difficulties concerned with the recognition of "dominant" species. It is with an appreciation of such difficulties and of the pitfalls involved in basing community structure on limited samples, that results from collections extending over 5 years have been drawn on to support and confirm the descriptions of the communities given here.

The observations of Orr (1954) on differences in distribution of certain flagellated organisms between the swamp drainage and the sewage drainage areas (Stations 1 and 4 of this study) are substantiated in the results. However, in the present study these phytoplankters made up a numerically small portion of the total number of organisms present at either of the stations. The greatest differences in community composition among sampling stations appeared in the results from the collection of February 1, 1956, made under 8 inches of ice. The per cent composition by algal divisions for the 5 stations for this collection are shown in Table II. The variation seen here is in marked contrast to the otherwise

TABLE II. Results from collection of February 1, 1956, showing variations in percentage composition of phytoplankton community under an ice cover.

| | Station 1 | Station 2 | Station 3 | Station 4 | Station 5 |
|---|---|---|---|---|---|
| Cyanophyta | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Chlorophyta | 10.9 | 35.9 | 71.2 | 89.2 | 52.1 |
| Chrysophyta | 86.9 | 52.2 | 26.5 | 8.8 | 25.0 |
| Euglenophyta | 1.1 | 4.3 | 1.4 | 2.0 | 2.1 |
| Pyrrophyta | 1.1 | 7.6 | 0.9 | 0.0 | 20.8 |

rather uniform distribution of dominant species over the remainder of the year. It is suggested that this diversity of community structure is in part a result of the presence of the ice cover and its interference with the normal mixing action of the wind.

Results indicate the presence throughout the entire season of the two species *Scenedesmus quadricauda* and *Pediastrum Boryanum*. There was, of course, an increase in numbers of these species along with other members of the green algal group in the spring and fall communities, but both species were common members of all other seasonal communities. It is sometimes difficult to distinguish, in the counting chamber, between living *Pediastrum* and empty-walled coenobia The latter were abundant in early winter and spring collections, particularly during turbulent periods, apparently being re-suspended from the shallow bottom. At all seasons, however, green-celled colonies could be found in the population. The same conditions were true to a lesser extent for *Scenedesmus*. It must be concluded that while the counts could conceivably include some "dead" or empty-celled colonies, living members of each genus were present in each collection throughout the season.

## SUMMARY

A study was made of seasonal variations in size and species composition of phytoplankton communities from 5 collecting stations in the highly productive Sanctuary Lake portion of Pymatuning Reservoir. Values for suspended organic materials concentrated by triple centrifugation ranged from 38.2 mg per liter to 3.6 mg per liter over a 14 month period.

General agreement was found between values for suspended organic materials determined by gravimetric procedures and for total cell numbers. Suspended inorganic materials were highest in the northern end of the lake where Linesville Creek contributes relatively high amounts of silt.

Community composition was essentially uniform among the 5 collecting stations over the period of the study with the exception of the communities developed under an ice cover. Here considerable variation was observed among the 5 sampling stations. It is suggested that these differences in community structure are a result of the interference of the ice cover with the normal mixing of the waters from the two distinct drainage areas.

Dominant species are listed for 5 seasonal phytoplankton communities. Summer communities are dominated by colonial Cyanophyta, spring and fall communities by Chlorophyta, and the winter community by combinations of Diatomaceae and Chlorophyta.

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# FLOWERING VARIATIONS IN *EUPATORIUM RUGOSUM*

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## INTRODUCTION

Transplant studies have shown that hereditary variations occur in many species. A source of differentiation in plants is the selective influence of climate. The aspect of climatically-controlled variants within a species was alluded to by Turresson (1922) who concluded that the species problem is in large measure ecological. As Went (1957, p. 96) suggested, it is necessary to study the behavior of ecotypes in relation to their environment to understand the climatically-selected variations that occur in a species. The presence

of a more or less continuous series of morphologically and ecologically intermediate populations often makes it impossible to define distinct ecotypes. Much of the variation in many species can probably be better described by the use of the term "cline" as defined by Huxley (1938). Clinal intraspecific differences are more likely in those species with wide ranges over which climatic change is gradual or continuous, whereas distinct ecotypes will be prevalent in diverse or discontinuous environments.

The effects of environment on differences within species of certain western North American plants were noted by Clausen, Keck, and Hiesey (1939, 1940). In uniform garden studies of 5 grass taxa in Nebraska, McMillan (1956a, 1956b) observed a clinal sequence in flowering from west to east. Larsen (1947) reported that eastern clones of *Andropogon scoparius* L. winter-killed in a common garden whereas western clones from the same latitude did not. For the same species, Cornelius (1947) stated that transplants from high latitudes initiated flowering earlier than those from farther south. Similar effects were reported by Goodwin (1941) in a study of *Solidago sempervirens* L. For *Eupatorium rugosum* Houtt., the white snakeroot, it was shown by Kucera (1958) that floral initiation and development in a uniform garden were related to the latitudinal source of wide-ranging populations and to the frost-free season. Colonies from the northern part of the range bloomed earlier than those from southern locations.

The present investigation was conducted to study further the effects of frost-free season on racial differentiation in *Eupatorium rugosum*, particularly as it relates to the east-west distribution. The effects of daylength on the flowering development of the species were also studied.

## Materials and Methods

Specimens of *Eupatorium rugosum* were grown in the greenhouse under varied light conditions from November, 1958, to June, 1959. Plants were grown from seeds from the following geographical locations:[1] Ontario, Canada; Richland Co., N. Dak.; Brookings Co., S. Dak.; Minnehaha Co., S. Dak.; Clay Co., S. Dak.; Litchfield Co., Conn.; Wayne Co., Mich.; Ingham Co., Mich.; White Co., Ga.; Butler Co., Mo.; and Douglas Co., Kan.

Ripened achenes from the current season of individual populations were planted in a sterilized medium consisting of 50% sand and 50% potting soil. Three seedlings of uniform size from each source were transplanted to 5 in. pots and given weekly applications of a full nutrient solution.

The transplants were grown for approximately 8 weeks and then divided into 3 lots and placed under 12, 14, and 16 hr light. Six to 9 plants from each source were used for each of the 3 photoperiods.

Each photoperiod chamber was 5 x 5 x 6 ft and placed over a greenhouse bench. It consisted of a wood frame around which was draped a removable black cloth. The top, made from heavy, black window shades, was permanently attached and provided an excellent shade during the day. Each light chamber was equipped with a 250 watt incandescent bulb controlled by a timer. These lights were suspended from an adjustable cord and placed 18 in. above the plants to provide a minimum reading of 1000 ft-c at the upper leaves. Artificial lights were used only to lengthen the light period to the desired time, and as a supplement on cloudy days. Temperatures throughout the experiment were approximately 20°C at night and 25-30°C during the day. Mechanical means of cooling the light chambers did not become necessary since lower night temperatures were maintained in the greenhouse as a whole.

Plants were observed closely for initial signs of flowering. The numerical system of Kucera (1958) for evaluating flowering development was used. The several stages of development and their assigned values are: vegetative, 0; flower buds small, inconspicious, observed only by separating uppermost pairs of leaves, 1; flower buds easily visible, 2; first disc flowers showing white corollas, 3; first flowers completely open, 4; full bloom, 5; flowers beginning to dry, 6; and flowers completely dried, achenes mature, 7. Daily observations of flowering development were made for 120 days. To determine the degree of development of flowering of each group on a particular date, the flowering score of individual plants was summed and divided by the total number of plants in the group. Plant height measurements and other observations were recorded at weekly intervals. These data provided a basis for appraising floral development of the plants in relation to the 3 photoperiods.

[1] Appreciation is expressed to Drs. O. A. Stevens (Univ. of N. Dak.), W. H. Duncan (Univ. of Ga.), K. C. Chambers (Osborne Laboratory), C. A. Taylor (S. Dak. State College), R. L. McGregor (Univ. of Kan.), B. Hayes (Detroit, Mich.), W. G. Dore (Ottawa, Can.), J. H. Beaman (Mich. State Univ.), T. Van Brugger (Univ. of S. Dak.), and to W. P. Hackbarth (Augustana College) for furnishing materials for this study.

TABLE I. Average score of the development of flowering of *Eupatorium rugosum* following 30, 60, 90, and 120 days under a 14 hr photoperiod.

| Seed Source | Latitude | Longitude | Elevation: Ft | Frost Free Season: Days | Numerical Score of Flowering[a] | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | 30 | 60 | 90 | 120 |
| Richland County, North Dakota (Wahpeton) | [b]46°16′N | 96°36′W | 962 | 129 | 2.9 | 3.6 | 5.4 | 7.0 |
| Ontario, Canada (Ottawa) | [c]45°24′N | 75°44′W | 260 | 142 | 2.4 | 3.4 | 5.1 | 6.3 |
| Brookings County, South Dakota (Brookings) | 44°20′N | 96°46′W | 1650 | 136 | 2.2 | 2.9 | 4.6 | 5.7 |
| Minnehaha County, South Dakota (Sioux Falls) | 43°34′N | 96°44′W | 1420 | 150 | 1.7 | 2.7 | 4.2 | 5.0 |
| Litchfield County, Connecticut (Cream Hill) | 41°52′N | 73°20′W | 1300 | 155 | 1.5 | 2.2 | 3.8 | 4.8 |
| Clay County, South Dakota (Vermillion) | 42°48′N | 96°56′W | 1220 | 160 | 1.2 | 1.9 | 3.4 | 4.8 |
| Ingham County, Michigan (East Lansing) | 42°44′N | 84°29′W | 856 | 158 | 0.7 | 1.8 | 3.2 | 4.6 |
| Wayne County, Michigan (Detroit) | 42°24′N | 83°00′W | 619 | 177 | 0.6 | 1.8 | 3.2 | 4.5 |
| White County, Georgia (Helen) | 34°42′N | 83°44′W | 1490 | 205 | 0 | 0 | 0.3 | 0.8 |
| Butler County, Missouri (Popular Bluff) | 36°45′N | 90°23′W | 332 | 191 | 0 | 0 | 0 | 0.3 |
| Douglas County, Kansas (Lawrence) | 38°58′N | 96°16′W | 1000 | 195 | 0 | 0 | 0 | 0 |

[a] An average based on 0—vegetative, 1—flower buds inconspicuous, 2—flower buds easily seen, 3—disc flowers showing white, 4—first flowers completely open, 5—full flower, 6—flowers beginning to dry, 7—achenes mature, flowers dried.
[b] Data for all United States stations from U.S.D.A. Yearbook of Agriculture "Climate and Man." 1941.
[c] Data for Canadian Station from Dominion Bureau of Statistics, "Canada Yearbook." 1956.

In addition to the greenhouse study, herbarium collections of white snakeroot plants were examined and data pertaining to floral development of each specimen were recorded.[2] Herbarium specimens representing collections from 35 states, the District of Columbia, and Canada were examined. By evaluating the data from these specimens, the sequence of flowering of white snakeroot plants in their native ranges could be ascertained.

White snakeroot plants from several geographical locations, growing in previously established plots at Columbia, Missouri, were also observed. Data collected from these specimens were compared with the results obtained from seed progeny tests and herbarium study.

## RESULTS

Flowering of white snakeroot plants was most successful at a 14 hr photoperiod. The plants grown at a 12 hr photoperiod flowered sporadically or not at all. For the 16 hr light period, growth response was accelerated while flowering response was retarded. However, floral buds were observed on a few plants after approximately 60 days and by the end of the experiment most of the plants had developed flower buds.

The average score of development of flowering of each geographic selection following 30, 60, 90, and 120 days at a 14 hr photoperiod is presented in Table I. These results show a trend in sequence of flowering from west to east. For example, at the 14 hr photoperiod, specimens from South Dakota were generally more advanced than those from Michigan. It was noted that progenies originating from the northern states were generally more advanced than those from the same general longtitude in the south.

The flowering behavior exhibited by white snakeroot stocks from different locations shows a continuous, or clinal, type of intraspecific variation. As shown in Table I, the numerical values of flowering overlap from one station to another, suggesting gradual climatic differentiation. The 6 to 9 individual plants used for each photoperiod which were averaged for the data given were uniform in their development except those at the 12 hr photoperiod. In only one station was a departure noted. The plant material from Douglas County, Kansas did not flower under any of the 3 photoperiods.

The continuous type of variation shown in Table I indicates a relationship to the frost-free

[2] Acknowledgement is given to the curators of the herbaria who furnished materials for this study. These are Drs. Lloyd Shinners (Southern Methodist Univ.), J. R. Millar (Chicago Natural History Museum), L. B. Smith (Smithsonian Institution), R. E. Woodson (Missouri Botanical Gardens), and R. K. Godfrey (Florida State Univ.).

season. Plants originating in short-season climates showed the earliest flowering. With increasing length of growing season flowering was later in the south and/or east in the overall patterns. Even though the sum effect of the total range studied indicates the above trends, a comparison of adjacent stations, or those with similar growing season, shows only minor or even opposite differences. These small variations or actual discrepancies suggest the need for studying numerous progenies in a graduated series from one environmental extreme to the other.

Plants grown at 12 hr light were stunted. Retarded growth was especially prevalent in the northern progenies. In contrast, specimens at the 16 hr photoperiod elongated rapidly and growth continued throughout the experiment. The 14 hr plants exhibited growth response intermediate between that of the 12 hr and 16 hr plants.

Data obtained from the herbarium study were in close agreement with those obtained from the experiments. Results presented in Table II show

TABLE II. Effect of longitude on flowering of *Eupatorium rugosum* as determined from herbarium specimens.

| Source[a] | Growing Season: Days[b] | No. of Herbarium Sheets Observed | Numerical score of Flowering[c] | Collection Period[d] |
|---|---|---|---|---|
| South Dakota | 146 | 5 | 6.1 | August |
| Massachusetts | 199 | 11 | 5.2 | September |
| Nebraska | 153 | 5 | 5.6 | August |
| Pennsylvania | 155 | 16 | 5.6 | September |
| Kansas | 177 | 5 | 5.5 | September |
| Virginia | 203 | 44 | 4.8 | Aug.-Oct. |
| Oklahoma | 216 | 3 | 4.3 | Aug.-Sept. |
| North Carolina | 222 | 16 | 4.8 | September |
| Texas | 256 | 13 | 4.1 | Sept.-Nov. |
| Florida | 290 | 19 | 4.0 | Oct.-Dec. |

[a] Each pair of states are approximate latitudinal equivalents.
[b] An average of growing seasons for those stations nearest localities indicated on herbarium vouchers, based on U. S. D. A. Yearbook, "Climate and Man," 1941.
[c] An average value of floral development for all herbarium specimens by states in relation to the period of collection. The value of 4.0 indicates the opening of the first disc flowers; 6.0, all flowers mature and drying.
[d] The predominant period of collection taken from herbarium specimens examined from each state.

that longitudinal variations in the overall pattern of floral development of white snakeroot plants do exist. In general, flowering was slower as the growing season became longer. A similar relationship was noted for plants growing in the outside garden.

## DISCUSSION

Adaptation of widespread populations of white snakeroot to regional differences in climate are indicated by variation in blooming under uniform conditions. In this study, the rate of flowering development closely paralleled a decreasing growing season. This general agreement, regardless of photoperiod, suggests that the time of flowering and rate of development is adapted to the length of the growing season.

The modifying effects of a decreasing growing season on photoperiodic response in nature were shown by the fact that on any given date progenies from midwestern states were generally more advanced in flowering than those from the same general latitudes in the east. If photoperiod were the only factor involved, we would expect both the eastern and the western progenies from the same general latitudes to flower simultaneously, since at any particular time the daylength would be the same for the two latitudinal equivalents. The fact that this did not occur, but that eastern progenies were generally later in floral initiation than corresponding western progenies, points to the length of the frost-free season as a major influence in producing adaptational differences within the species. The western specimens not only initiated flowering earlier than those from the east, but they also developed more rapidly. The earlier flowering development of progenies from westerly locations indicates that relative precocity is probably adaptive under conditions of shorter growing seasons. The selective advantage of early maturity seems less critical in the longer growing seasons farther east. The adaptation of species to length of growing season has also been suggested by McMillan (1956a, 1956b). In uniform garden studies of several grass taxa in Nebraska, he noted a clinal sequence in blooming from west to east. A shorter growing season in western Nebraska than in the eastern part of the state was given as one reason for the observed variations in flowering.

On the basis of earlier flowering of western specimens, it is suggested that floral initiation in native habitats occurs under a longer daylength than in those from farther east. In this respect, western plants may react physiologically like northern ones. This was also shown in Larsen's work (1947) in which northern strains of *Andropogon* flowered at a 15 hr day but were inhibited at a 13 and 14 hr day, whereas southern clones flowered at a 14 hr photoperiod but did not flower at a 15 hr day. An eastern strain from North Carolina, latitude 36°00′, which flowered at a 14 hr day, winter killed; but an Oklahoma strain, latitude 36°10′, which did not winter-kill in a common garden, flowered at 15 hr of light.

In view of these results, it is apparent that Hopkins' Bio-climatic Law does not apply to

geographical races of white snakeroot as it relates to longitude. According to the law, the summer and fall development of a species in temperate North America is 4 days later for each 5 degrees of longitude toward the west. It has been shown that flowering response of white snakeroot is closely related to length of the frost-free period. Since this period is shorter in the Midwest than farther east, the western progenies initiate flowering earlier. Consequently, the Bioclimatic Law should be reversed in respect to longitude, at least in its application to the fall-blooming white snakeroot.

White snakeroot plants under observed conditions showed a definite, although gradual, sequence of flowering at a 14 hr photoperiod, with flowering generally more advanced in the direction of increasing latitude of their source. In this respect, these results agree with those obtained earlier (Kucera 1958). The variation in flowering response to a single photoperiod of various geographical selections of the species suggests that hereditary factors may bring about this phenomenon. The hereditary control of flowering in geographical races of white snakeroot was further observed in specimens grown in the uniform garden on the campus of the University of Missouri. Specimens in this garden, which includes several geographical selections, exhibited the same sequence of flowering as those grown experimentally at a 14 hr photoperiod. The fact that the sequence of flowering was the same for both the experimental plants and the uniform garden plants tends to confirm that these variations in flowering are adaptive to climatically different regions.

The general flowering response to a single photoperiod of white snakeroot plants from climatically different regions, suggests that species tolerance encompasses a wide range of physical conditions. The question arises as to whether the photoperiod itself is a major influencing factor or whether it is secondary in its effects, perhaps modifying other environmental factors which directly affect the plants. This question is particularly pertinent, since under observed conditions progenies from almost every source showed signs of flowering at a 16 hr photoperiod as well as a 14 hr light period by the end of this investigation. However, the plants grown at a 12 hr daylength were stunted and many died before the end of this study. Flowering in this group was sporadic and unpredictable, indicating the necessity for a minimum photoperiod of more than 12 hr for normal development. On the other hand, the 16 hr plants continued relatively rapid vegetative growth throughout the experiment, with flowering delayed until later. Specimens grown at 14 hr light were intermediate in growth response and flowering. According to Went (1948), different processes occur during the light and dark periods and those processes must be balanced to obtain specific responses. Therefore, a physiological balance between photosynthesis and respiration in which there is an excess of photosynthate over the products respired, must occur for normal reproductive and vegetative development. From this, it appears that a 14 hr photoperiod most nearly approximates the optimum daylength for white snakeroot, under conditions of this experiment.

In its natural environment, however, white snakeroot is not subjected to a constant light period throughout its life cycle. Consequently, it is probable that the species in nature has adapted itself not to uniform diurnal periods of light but to continuously changing ones. Apropos of this, Whyte and Oljhovikov (1939) showed that in a large number of plants, floral initiation occurs under one day length but flowering becomes manifest under a different one. From this and similar instances, it is suggested that the reproductive processes of many species are not as closely adapted to a specific day length as is often inferred. However, histological studies will be necessary to ascertain the exact relationship between photoperiod and floral initiation in white snakeroot.

Increasing elevation from the Atlantic seaboard westward into the interior of the continent is suggested as a factor in the adaptive flowering response of white snakeroot in relation to longitude. This is based on the principle that increasing elevation produces a more severe climate and therefore decreases the frost-free season. In addition, the prevailing climate of the Midwest is generally more fluctuating than the climate farther east because of the great distance of the midwestern states from large bodies of water. The prevailing winds are also involved. The coastal area is blanketed with warmer air from the Atlantic Ocean and the Gulf of Mexico, while the midwestern states are subjected to more continental extremes from the north and northwest.

Lack of flowering response of white snakeroot progenies from Douglas County, Kansas may have been the result of local environmental factors. Local conditions may exist which modify the environment of the site from which the plants

were obtained, possibly increasing the growing season to more than 195 days. If this were so, we would not expect flowering to occur under the conditions of this study. Another consideration is the perennial habit of white snakeroot. Like many perennials, this particular population may require more than one season to mature, in which case flowering would not have occurred.

On the basis of geographical location and the 14 day difference in frost-free season (Table I), plants from White County, Georgia, might be expected to flower later than those from Butler County, Missouri; however, this was not observed. The fact that specimens from both locations were similar in flowering response may also suggest microhabitat effects not revealed by general climatic data. Additional study is needed to gauge the effects of local habitat on species differentiation.

Results of this study indicate that flowering patterns in white snakeroot over its broad range are the result of climatic selection. Adaptation to varying lengths of frost-free period and response to day length are important factors in racial differentiation.

## Summary

A greenhouse experiment was conducted at Columbia, Missouri to observe flowering behavior of wide-ranging collections of white snakeroot, *Eupatorium rugosum,* under uniform conditions. Selections were obtained from North Dakota, South Dakota, Connecticut, Michigan, Georgia, Missouri, Kansas, and Ontario, Canada. Three photoperiods, 12, 14, and 16 hr were employed.

Results indicated that flowering was most successful at 14 hr light. Under this condition, flowering was earliest in western plants and progressively later for eastern plants at the same latitude. At the same longitude, northern specimens flowered earlier in comparison to those farther south. Plants grown at a 12 hr day length were stunted and flowered sporadically. No predictable sequence of flowering was noted. At 16 hr day length, plants continued rapid vegetative growth, developing flower buds after approximately 100 days of treatment. However, development of flowering was earliest in northern and western stocks and progressively later in plants from farther south and east.

It is suggested that the time of flowering and the rate of development are closely associated with the frost-free season. Plants from western sources have become adapted to a more continental climate, with accompanying shortening of the growing season, and react physiologically similar to northern specimens. Earlier flowering development in western and northern plants is probably adaptive to shorter seasons. Broad species tolerance of photoperiod conditions suggests the means by which racial adjustment to a particular set of climatic conditions is secured.

The effects of longtitude on flowering development in white snakeroot collections proved to be an exception to the general principle of the Bioclimatic law, which states that fall flowering progresses from east to west.

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# COMPARISON OF THE PRESENT VEGETATION WITH POLLEN-SPECTRA IN SURFACE SAMPLES FROM BROWNINGTON POND, VERMONT

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## INTRODUCTION

Pollen-bearing sediments found in lakes or bogs provide a record of past vegetation, presumably arranged in a stratigraphic column. Many pollen deposits contain essentially the same pollen types throughout. Thus description of a deposit depends largely upon a quantitative determination of the relative proportions of pollen types at various levels. Interpretation of pollen deposits assumes that frequencies of pollen types deposited reflect the complexion of the surrounding vegetation. Therefore, changes in frequencies of pollen types within the stratigraphic column are assumed to reflect changes in proportions of species or genera in the surrounding vegetation. These changes are often interpreted as the result of climatic change, one of the major factors affecting species composition of vegetation. For this reason, interpretations of pollen-bearing deposits are of great interest to students in such fields as glacial geology and paleoclimatology.

It has long been recognized, however, that the efficiency of pollen production and dispersal in different species of plants varies widely. A reasonable interpretation of a pollen spectrum can be made only if the relative pollen dissemination efficiency of each species is known. Attempts to estimate pollen production and pollen dispersal distance have been made in Europe (reviewed by Faegri and Iversen 1950) and in Japan (e.g. Tsukada 1958), but research in this aspect of pollen analysis has been largely neglected in North America. Pollen analysts here have tended to rely on European estimates of pollen production, a dangerous practice because the pollen production of congeneric species has been shown to vary (Pohl 1937). In a few areas, the present vegetation, studied at least in part quantitatively, has been compared to the pollen spectra in surface moss polsters or lake muds: the Great Smoky Mountains (Carroll 1943), Oregon (Hansen 1949), Alaska (Livingstone 1955), Alberta (Erdtman 1943) and Quebec (Potzger *et al.* 1956). However, pollen dissemination characteristics of most forest trees of New England are completely unknown.

This paper compares the present vegetation of the Memphremagog quadrangle in northern Vermont, an area containing both deciduous and coniferous tree species, with pollen spectra in samples of bottom muds now forming in lakes in that area. It describes 1) the methods and results of a survey of the vegetation of the quadrangle, 2) the methods and results of pollen analysis of mud samples, and 3) a comparison between these data. From the results a rough estimate is made of the relative pollen dissemination efficiency of some of the more common forest trees of the region. The significance of the results for the interpretation of fossil pollen spectra is discussed.

Colloquial names for tree species will be used in the discussion. For the convenience of the reader, a list of the names and their Latin equivalents (Fernald 1950) is given below:

| | |
|---|---|
| Alder | *Alnus* spp. |
| Black alder | *Ilex verticillata* |
| Apple | *Pyrus Malus* |
| Arbor vitae | *Thuja occidentalis* |
| Black ash | *Fraxinus nigra* |
| White ash | *Fraxinus americana* |
| Mountain ash | *Pyrus americana* |
| Large-toothed aspen | *Populus grandidentata* |
| Trembling aspen | *Populus tremuloides* |
| Beech | *Fagus grandifolia* |
| Gray birch | *Betula populifolia* |
| Paper birch | *Betula papyrifera* |
| Yellow birch | *Betula lutea* |
| Butternut | *Juglans cinerea* |
| Black Cherry | *Prunus serotina* |
| Pin-cherry | *Prunus pensylvanica* |
| Chestnut | *Castanea dentata* |
| Elm | *Ulmus americana* |
| Balsam fir | *Abies balsamea* |
| Hawthorn | *Crataegus* spp. |
| Hemlock | *Tsuga canadensis* |
| Hickory | *Carya* spp. |
| Hop-hornbeam | *Ostrya virginiana* |
| Larch | *Larix laricina* |
| Mountain maple | *Acer spicatum* |
| Red Maple | *Acer rubrum* |
| Striped maple | *Acer pensylvanicum* |
| Sugar maple | *Acer saccharum* |

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Red Oak ..... *Quercus rubra*
Red pine ..... *Pinus resinosa*
White pine ..... *Pinus Strobus*
Balsam poplar ..... *Populus balsamifera*
Shadbush ..... *Amelanchier*
Black spruce ..... *Picea mariana*
Red spruce ..... *Picea rubens*
White spruce ..... *Picea glauca*
Poison sumac ..... *Rhus Vernix*
Willow ..... *Salix* spp.

## Geology and Climate of the Memphremagog Quadrangle

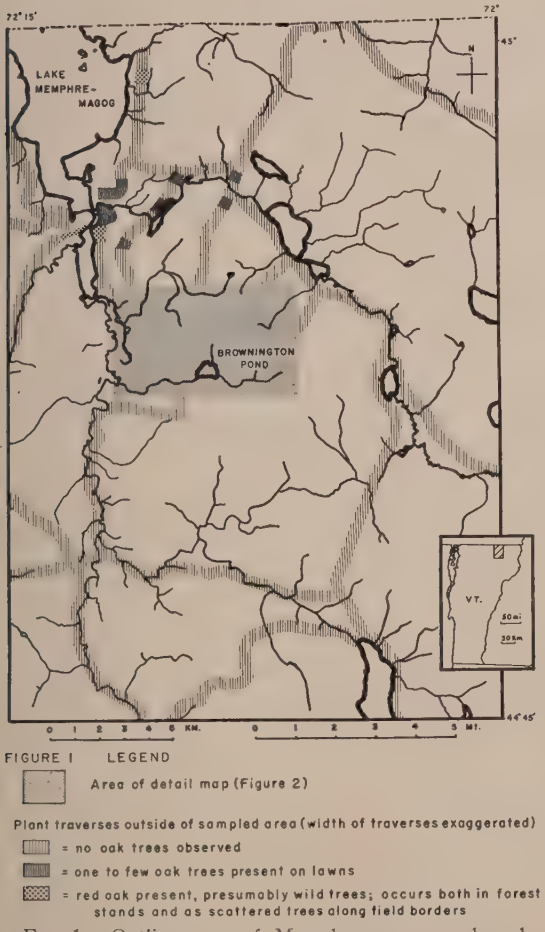
72°15'
72°
45°
LAKE MEMPHREMAGOG
N
BROWNINGTON POND
VT.
50 mi
205 m
44°45'
0 1 2 3 4 5 KM.
0 1 2 3 4 5 MI.
FIGURE 1 LEGEND
Area of detail map (Figure 2)
Plant traverses outside of sampled area (width of traverses exaggerated)
= no oak trees observed
= one to few oak trees present on lawns
= red oak present, presumably wild trees; occurs both in forest stands and as scattered trees along field borders

Fig. 1. Outline map of Memphremagog quadrangle, showing the distribution of oak. Inset shows location of Memphremagog quadrangle (hachured area) in Vermont. Map is drawn from U. S. Geological Survey topographic map, 1:62,500.

The Memphremagog quadrangle (Fig. 1) comprises rolling hills underlain in large part by phyllite, schist, quartzite, slate and limestone and rising 300-500 ft above adjacent valleys (Doll 1951). Altitudes range from 682 ft at Lake Memphremagog to 2935 ft, the summit of Goodwin Mountain. This peak and Barton Mountain are underlain by granite and lie near the southern edge of the quadrangle. Granite also underlies a circular area about 5 miles in diameter that extends northward from Brownington Pond. The principal drainage is northwestward toward Lake Memphremagog and thence to the St. Lawrence River. Most of the region is mantled with calcareous drift or "boulder clay." Sand and gravel deposits lie in many valleys. The uplands have slopes that are commonly less than 20%; many are less than 12%. The region has a continental climate with cold winters. The mean January temperature at Newport, on the southern shores of Lake Memphremagog, for the years 1930-1958 has been 15.7°F; the mean July temperature 67.2°F; and the average annual precipitation 35.7 in. (M. W. Drew, personal communication).

## Vegetation

Forests of sugar maple, birch, hemlock, beech and other deciduous species with occasional spruce, fir and arbor vitae occur on many slopes and on the summits of the hills and ridges. Stands of coniferous trees are common on the lower slopes and in the valleys. Young arbor vitae, spruce, fir and larch are frequently found in meadows and pastures. Apparently many of the coniferous stands are the first generation of trees on abandoned fields. This may explain their distribution in the valleys and on the gentler slopes that were suitable for clearing and cultivation.

Most of the cleared land in the quadrangle is used as pasture for dairy cattle. In addition, many of the forests show evidence of grazing by cattle and selective lumbering. The percentages of forested and non-forested land were estimated from the green overprint on the topographic map of the Memphremagog quadrangle, published by the U. S. Geological survey (scale 1:62,500, revised 1953). The quadrangle contains about 50% forested land, 45% non-forested land, and 5% open water.

A quantative study was made of the forests in the vicinity of Brownington Pond, near the center of the quadrangle. Sampling points within a 2 mile radius of the pond were selected by superimposing a ½ in. grid on the map. Points that fell in green areas were located on the ground by inspection of the topographic map. Because of limited time we sampled only at the 18 forested points within the northern 180° sector (Fig. 2). However, it is our impression, derived from traverses based upon

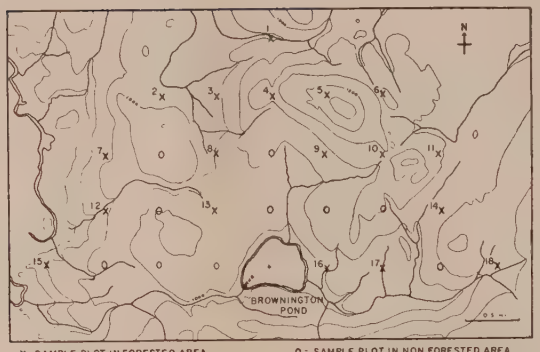
N
BROWNINGTON POND
X = SAMPLE PLOT IN FORESTED AREA
O = SAMPLE PLOT IN NON FORESTED AREA
• = SITE OF COLLECTION OF SEDIMENT SAMPLE

FIG. 2. Detail map of sample area, drawn from U. S. Geological Survey topographic map of the Memphremagog quadrangle. Contour interval 100 ft.

the road net (Fig. 1), that the vegetation in this sector is typical of much of the forest vegetation of the quadrangle. At each of the 18 sample points a circular 0.2 acre (8712 ft², about 800 m²) plot was marked off. All stems in the plot greater than 1 in. dbh (measured uniformly at 4.5 ft above the ground surface) were identified, measured with calipers, and tabulated in the following categories: 1-2, 2-3, 3-4, 4-5, 5-6, 6-10, 10-20 in. dbh. Stems greater than 20 in. dbh were measured and recorded individually. At sample point 3, saplings were so numerous that an estimate, rather than a count, was made for the deciduous tree stems in the smaller size categories. The data were later converted to basal area (cross-sectional area of stem at breast-height). Basal area is a more meaningful expression of the data for this study than stem frequency, because larger trees which have larger and higher crowns and presumably shed more pollen are assigned greater values than smaller trees. The total basal area of each sample plot, the number of stems counted, and the percentage of the total basal area contributed by each species are given in Table I and Figure 3. Spruce species were identified in the field by cone characters, but when cones were not available identifications were based on less reliable vegetative characters. For this reason spruce is identified only to genus in Figure 3.

Sample plots indicated a highly diverse forest cover (Fig. 3 and Table I). The number of tree species per plot ranged from 4-14. Of the 31 species recorded, only 8 were found in as many as half of the 18 plots, and 9 species were found in only one or 2 plots. Not one of the species was found in all plots, although yellow birch and balsam fir each occurred in all but 3. Only 5 species (balsam fir, arbor vitae, sugar maple, spruce and balsam poplar) constituted as much as 50% of

TABLE I. Total basal area of each plot, the number of stems counted, and the percentage of basal area in sample plots contributed by species not shown in Fig. 3.

| Sample plot no. | Total basal area in plot in ft² | Total number stems in plot | Percentage basal area in plot: |
|---|---|---|---|
| 1 | 42.05 | 99 | |
| 2 | 33.31 | 183 | Pin-cherry 0.04; apple 1.28 |
| 3 | 13.62 | 421 | Pin-cherry 3.40 |
| 4 | 15.32 | 148 | White pine 1.07; hawthorn 0.74 |
| 5 | 25.71 | 63 | Striped maple 1.67 |
| 6 | 26.16 | 71 | Striped maple 8.45 |
| 7 | 19.74 | 326 | Paper birch 10.20; apple 1.67; shadbush 0.06 |
| 8 | 21.03 | 170 | Striped maple 0.81 |
| 9 | 30.50 | 311 | Willow 0.19; black alder 4.92 |
| 10 | 14.86 | 112 | Striped maple 0.25; black ash 7.73 |
| 11 | 21.15 | 125 | Striped maple 0.32; pin-cherry 0.52; apple 0.06 |
| 12 | 19.22 | 139 | Black ash 0.41; pin-cherry 4.94; alder 3.32; shadbush 0.13; poison sumac 0.06 |
| 13 | 27.72 | 199 | |
| 14 | 15.13 | 68 | |
| 15 | 20.27 | 156 | Paper birch 0.87 |
| 16 | 33.28 | 135 | Alder 0.75; shadbush 0.10 |
| 17 | 7.12 | 153 | Paper birch 0.34; willow 5.75; pin-cherry 0.86; mountain ash 0.52 |
| 18 | 23.34 | 97 | Black cherry 1.49 |

the basal area in any one plot. Stand diversity can be illustrated by another means. If the species found in each sample plot are arranged in descending order of basal area, and the minimum number of species required to make 75% of the basal area in the plot is recorded, it will be seen that the composition of no 2 plots is the same. The number of species required ranges from 1-4. Sugar maple provides the largest percentage of basal area in 5 plots, and spruce, arbor vitae, and hemlock in 2 plots each. In terms of total basal area in all 18 sample plots (Table II), the most abundant trees are the maples, arbor vitae, balsam fir, and the spruces, in that order. Each of these constitutes more than 10% of the total basal area.

Red pine, butternut, large-toothed aspen and oak trees were observed in the Memphremagog quadrangle, although none of these species was found at the sample points. Butternut trees were seen in field borders immediately north of the sample area, large-toothed aspen were seen on a few steep slopes, and red pines occasionally were observed on thick deposits of sand and gravel. Oak trees are apparently extremely rare in the Memphremagog area (Fig. 1). A few red oaks, and one mossy-cup oak (*Quercus macrocarpa*) were seen near farmhouses and in the villages. Red oaks are common shade trees in the city of Newport. Forest stands containing red oak trees were observed only on the steep sand banks, 200-400 ft high, adjacent to South Bay of Lake

FIG. 3. Percentage of basal area in sample plots contributed by each species. Only those species that contributed at least 15 per cent of the basal area of one or more plots are shown.

Memphremagog, where at least 50% of the trees are red oaks. Other species are red pine, white pine, large-toothed aspen, trembling aspen, balsam poplar, red maple, sugar maple, striped maple, gray birch, paper birch, balsam fir, and arbor vitae. No oak was seen on the less extensive sand and gravel deposits along the rivers, or on steep, thinly-mantled bedrock slopes. Apparently oak does not grow naturally in this region except on coarse-grained, gravelly soils on extremely steep slopes. However, the possibility exists that steep slopes on higher hills in the southeastern part of the quadrangle, which were not thoroughly examined, support forest containing oak trees.

Of the tree species not found in any vegetation samples, oak is of the greatest interest because its pollen is found in all the surface samples, where it constitutes from 2.1-3.6% of the tree and shrub pollen. Only 8 of the tree and shrub pollen types exceed this maximum frequency of oak. Studies of the distribution of oak in New England (Goodlett, in preparation) suggest that oak is essentially absent from a wide area around Lake Memphremagog (Fig. 4). Unfortunately, the local distribution of oak in southern Quebec is not known, although small-scale distribution maps (Munns 1938; Little 1949) indicate that it is present.

Sample plots in unforested areas were not studied quantitatively. Four of them lay in meadows, one in a meadow with a few elm, 4 in meadows with young arbor vitae, spruce and fir, and one in a meadow overgrown with shrubs, young conifers and young deciduous trees.

## POLLEN ANALYSIS OF LAKE MUD

Samples for pollen analysis were collected from Brownington Pond in the Memphremagog quadrangle and from Spectacle Pond, 15.5 miles to the southeast, in the Island Pond quadrangle. Samples #1-5 were collected from the surface of the mud bottom in the shallower parts of

TABLE II. Comparison of percentages of total basal area in the sample plots and percentages of pollen in the sediment samples.

| | | Brownington Pond | | | | | | Spectacle Pond |
|---|---|---|---|---|---|---|---|---|
| Surface sample no. | | #1 | #2 | #3 | #4 | #5 | #6 | #10 |
| Percentage total basal area: | | Percentage tree and shrub pollen: | | | | | | |
| Sugar maple 16.86<br>Striped maple 0.71 | 17.57 | 3.88 | 2.05 | 2.69 | 4.03 | 3.46 | 3.27 | 1.71 |
| Arbor vitae | 15.91 | 1.44 | 1.56 | 0.63 | 0.82 | 3.74 | 4.48 | 1.71 |
| Red spruce 6.31?<br>White spruce 3.97?<br>Black spruce 0.71?<br>Unidentified spruce 0.31 | 11.33 | 3.70 | 3.78 | 2.24 | 4.12 | 5.20 | 6.54 | 7.58 |
| Yellow birch 6.16<br>Gray birch 2.10<br>Paper birch 0.54 | 8.80 | 53.61 | 55.83 | 57.65 | 56.87 | 50.68 | 48.92 | 49.86 |
| Balsam poplar 4.18<br>Trembling aspen 3.56<br>Large-toothed aspen — | 7.74 | 0.09 | 0.25 | 0.09 | 0.27 | 0.09 | 0.32 | 0.76 |
| Hemlock | 5.48 | 9.39 | 8.46 | 9.40 | 8.97 | 7.75 | 6.78 | 1.71 |
| Beech | 4.52 | 5.87 | 6.90 | 10.38 | 8.24 | 9.21 | 6.70 | 5.12 |
| White ash 2.39<br>Black ash 0.50 | 2.89 | 2.08 | 1.40 | 0.80 | 1.83 | 2.46 | 1.44 | 1.71 |
| Red maple | 2.79 | 0.36 | 0.33 | 0.27 | 0.09 | 0.36 | 0.47 | — |
| Basswood | 2.79 | — | 0.16 | 0.27 | 0.09 | 0.09 | — | 0.09 |
| Larch | 2.40 | — | — | — | — | 0.09 | — | — |
| Elm | 2.39 | 2.08 | 1.89 | 1.07 | 1.83 | 1.37 | 2.71 | 1.42 |
| Hop-hornbeam | 2.09 | 1.35 | 1.48 | 1.43 | 1.37 | 1.00 | 0 88 | 1.23 |
| Pin-cherry 0.39<br>Apple 0.19<br>Black cherry 0.08<br>Hawthorn 0.03<br>Shadbush 0.01<br>Mountain ash 0.01 | 0.71 | 0.19 | 0.33 | — | 0.45 | — | 0 08 | 0.47 |
| Black alder | 0.37 | — | — | — | — | — | — | 0.28 |
| Alder | 0.22 | 3.07 | 4.43 | 2.06 | 2.11 | 3.01 | 4.23 | 7.87 |
| Willow | 0.11 | 0.36 | 0.25 | 0.09 | 0.27 | 0.18 | 0.32 | 0.28 |
| Mountain maple | 0.07 | — | — | — | — | — | | — |
| Poison sumac | 0.003 | — | — | — | — | — | . | — |
| White pine 0.04<br>Red pine — | 0.04 | 6.86 | 6.16 | 5.82 | 4.85 | 6.20 | 8.22 | 12.04 |
| Oak — | | 3.16 | 2.47 | 3.58 | 2.93 | 2.92 | 2.40 | 2.08 |
| Hickory — | | 0.09 | 0.33 | — | 0.18 | 0.18 | 0.32 | 0.09 |
| Butternut — | | 0.18 | 0.16 | 0.45 | 0.09 | — | 0.32 | 0.28 |
| Chestnut — | | 0.09 | 0.08 | 0.09 | 0.09 | 0.09 | 0.08 | — |
| Hazel — | | 0.09 | 0.16 | — | — | 0.09 | — | 0.19 |
| *Viburnum* — | | — | — | 0.09 | — | 0.09 | | — |
| *Ericaceae* — | | — | 0.16 | — | — | — | — | 0.19 |
| *Myricaceae* — | | 0.45 | 0.41 | 0.27 | 0.27 | 0.45 | 0.49 | 2.08 |
| Total basal area in sample plots 409.53 ft² | | | | | | | | |
| Total number stems counted in sample plots—2976 | | | | | | | | |
| Number tree and shrub pollen counted | | 1148 | 1218 | 1117 | 1092 | 1097 | 1253 | 1055 |
| Distance from shore in feet | | 50 | 55 | 225 | 400 | 700 | 1600 | 250 |
| Water depth in feet | | 0.5 | 1 | 1.5 | 3 | 4.5 | 25 | 7 |

Brownington Pond and sample #10 was collected from the surface of the mud bottom in Spectacle Pond. The samples were collected directly from the mud surface in 5 dr glass vials. The approximate distance from shore at which the samples were taken and the water depth at each sampling site are indicated in Table II.

Sample #6, mud from the center of Brownington Pond, was collected with a Livingstone borer by Davis and E. S. Deevey Jr. Soundings indicated a firm mud bottom 8 m (26 ft) below the water surface. The borer was lowered through the water to a depth of 7.3 m and a core of water and mud was taken from 7.3 m-8.3 m depth. A few minutes after the liner containing the core was brought to the surface, it was tilted to pour off water and loose mud in the upper part of the liner. The mud was caught in numbered 5 dr vials as it was poured. These samples were designated #6-9. The similarity of pollen frequencies in these samples indicated that mixing might have occurred when mud samples were poured from the liner. However, when they were tested for similarity by the chi-square test recommended by Faegri and Ottestad (Faegri and Iversen 1950), it was found that the frequencies of spruce, hemlock, birch and ash pollen in the 4 samples varied more than could be expected on the basis of chance if all 4 were from the same population ($0.05>P$). The frequencies of spruce, hemlock and ash pollen in the 2 samples, #6 and #7, also varied significantly. It was decided, therefore, that complete mixing had not occurred, and that sample #6, although perhaps contaminated to some extent with slightly older material, could be considered a sample of the mud surface.

Pollen was extracted from mud samples by flotation in bromoform (Frey 1951), deflocculation for 6 min. with 10% KOH in a boiling water bath, and acetolysis as described by Faegri and Iversen (1950). The residue was stained with neutral red and mounted in Mounting Medium No. 8, obtained from the Tanglefoot Co., Grand Rapids, Mich. Pollen counts were made at 200x magnification. An apochromatic oil immersion lens was used for all critical identifications, including that of oak pollen. Pollen identifications were based on comparison with reference slides from herbarium collections. At least 1000 tree and shrub pollen grains were counted in each sample. The sum for calculating the percentages of these pollen types included only tree and shrub (and unidentified *Rosaceae*) pollen to allow comparison of pollen frequencies with frequencies of trees and shrubs in the forest survey. Percentages of herbaceous and aquatic plant pollen and spores were calculated as percentages of total tree, shrub and terrestrial herb pollen. The results of the analyses are shown in Tables II and III.

*Pollen size as a means of identification.*—Size measurements of birch, pine and spruce pollen in the sediment samples were made because size measurements are sometimes used for species identification of pollen types identifiable otherwise only to genus. The usual practice has been

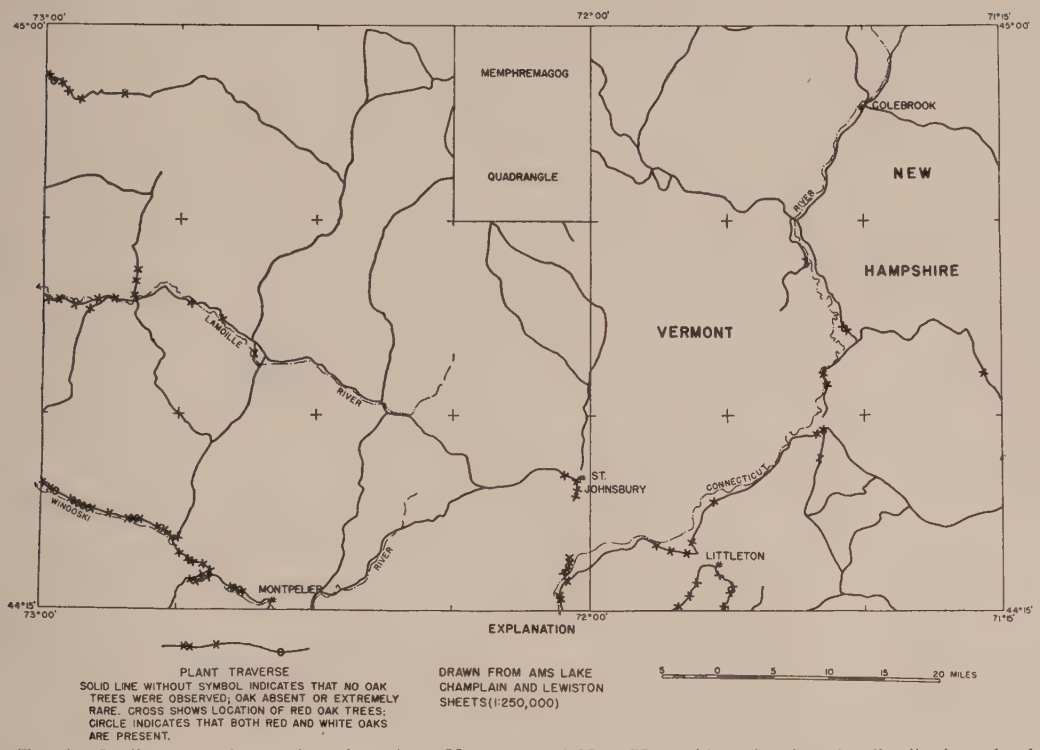


FIG. 4. Outline map of a portion of northern Vermont and New Hampshire, showing the distribution of oak in the region surrounding the Memphremagog quadrangle.

to compare the size distribution of a fossil pollen type with the size distribution observed in pollen prepared from living trees or herbarium specimens. Because size distributions of pollen from a single plant or from several plants of the same species are unimodal, bimodal size distributions of fossil pollen are usually interpreted to indicate the presence of pollen contributed by at least 2 species within the genus. The modal sizes are compared to the mean sizes of pollen observed in modern species, and identifications are made on this basis (Cain and Cain 1948). It was felt that the validity of this method could be tested by comparing the distributions of pollen size in the sediment surface samples with the mean pollen sizes described in the literature for species now living in the region.

The species of birch known in the Memphremagog quadrangle are yellow birch, gray birch and paper birch. In the sample plots yellow birch makes up to 70% of the basal area recorded for birch, gray birch 24%, and paper birch 6%. The mean size of pollen, treated with KOH and acetolyzed, observed for these species is 29.7μ (the average of the mean sizes of 100 grains measured in each of 10 collections from herbarium specimens) for yellow birch, 30.7μ (5 collections) for paper birch, and 25.4μ (4 collections) for gray birch (Leopold 1956). The birch pollen in our samples #1 and #6 is considerably smaller (Fig. 5). It ranges from 14.8μ to 29.6μ; the modal size is 24.7μ. Probably the pollen in the sediments is pollen from the 3 local species that has undergone a change in size as a result of laboratory treatment or of conditions of preservation. This hypothesis is supported by the fact that the pine and spruce pollen in the sediments is considerably smaller than modern pine and spruce pollen (see below). The mode of the size distribution of birch pollen in samples #1 and #6 may represent the modal size of yellow and paper birch pollen, and the asymmetry of the distribution may be due to the presence of gray birch pollen with a smaller modal size. In these samples, comparison of absolute pollen size apparently is not a reliable method for making species identifications.

White pine and red pine were the only pine species observed in the Memphremagog quadrangle. Measurements of the maximum internal diameter of acetolyzed pine pollen have been made by Cain and Cain (1948). They report

TABLE III. Percentages of non-arboreal pollen types in the sediment analysis.

| | Brownington Pond | | | | | | Spectacle Pond |
|---|---|---|---|---|---|---|---|
| Surface sample no. | #1 | #2 | #3 | #4 | #5 | #6 | #10 |
| | Percent total terrestrial plant pollen: | | | | | | |
| Total herbs | 9.92 | 6.19 | 6.92 | 8.16 | 10.16 | 16.19 | 13.60 |
| Total shrubs | 3.58 | 3.76 | 2.33 | 2.44 | 3.44 | 4.15 | 9.42 |
| Total NAP | 13.50 | 9.95 | 9.25 | 10.60 | 13.60 | 20.33 | 23.01 |
| *Gramineae* | 3.66 | 3.39 | 1.82 | 3.20 | 4.01 | 6.35 | 6.06 |
| *Cyperaceae* | 2.11 | 1.62 | 0.67 | 0.67 | 0.57 | 1.54 | 0.90 |
| *Ambrosia* | 2.20 | 3.02 | 0.23 | 1.85 | 3.28 | 4.75 | 3.28 |
| *Xanthium*-type | — | 0.07 | — | 0.25 | — | 0.07 | — |
| *Artemisia*-type | 0.08 | 0.07 | 0.25 | 0.08 | 0.24 | 0.20 | 0.16 |
| *Tubuliflorae* | 0.24 | 0.37 | — | 0.25 | 0.24 | 0.60 | 0.16 |
| *Liguliflorae* | — | — | 0.08 | — | 0.08 | 0.07 | 0.16 |
| *Chenopodiaceae* | 0.16 | 0.22 | — | 0.17 | — | 0.13 | 0.16 |
| *Rumex* | 1.30 | 1.18 | 1.33 | 1.26 | 1.39 | 1.81 | 2.05 |
| *Plantago major*-type | 0.08 | — | — | — | 0.16 | 0.20 | — |
| *Plantago lanceolata*-type | — | 0.15 | — | — | 0.08 | 0.07 | 0.16 |
| *Plantago* sp. | — | — | — | — | — | 0.13 | — |
| *Thalictrum* | 0.16 | — | — | 0.17 | — | 0.07 | 0.24 |
| *Caryophyllaceae* | — | 0.07 | — | — | — | 0.13 | — |
| *Leguminosae* | — | 0.07 | 0.17 | — | — | — | 0.08 |
| *Umbelliferae* | — | — | 0.08 | — | — | — | 0.08 |
| *Urticaceae* | — | — | — | — | 0.08 | 0.07 | — |
| *Galium*-type | — | — | — | — | — | — | 0.08 |
| Number terrestrial plant pollen counted | 1230 | 1357 | 1200 | 1189 | 1221 | 1495 | 1221 |
| Not included in sum: | | | | | | | |
| Unknown | 0.24 | 0.07 | 0.58 | 0.75 | 0.08 | 0.60 | 0.57 |
| *Ranunculaceae* | 0.16 | — | 0.17 | 0.08 | 0.41 | 0.40 | 0.33 |
| *Typhaceae* | — | 0.07 | 0.08 | 0.25 | 0.16 | — | 0.33 |
| *Nymphaea* | 0.08 | — | — | — | — | 0.07 | — |
| *Nuphar* | 0.08 | 0.07 | — | 0.17 | 0.24 | 0.13 | 0.08 |
| *Pontederia* | 0.08 | — | 0.08 | 0.08 | 0.08 | 0.13 | — |
| *Potamogeton* | 0.08 | 0.15 | 0.08 | 0.08 | 0.08 | 0.07 | 0.08 |
| *Brasenia* | — | 0.07 | — | — | — | — | — |
| *Myriophyllum* | — | — | 0.08 | 0.08 | 0.08 | 0.07 | — |
| *Lycopodium* | 0.41 | 0.22 | 0.58 | 0.17 | 0.24 | 0.67 | 0.74 |
| *Lycopodium lucidulum*-type | 0.16 | 0.22 | 0.17 | 0.25 | 0.08 | 0.40 | 0.49 |
| *Selaginella* | — | — | — | — | — | 0.07 | — |
| *Isoetes* | — | — | 0.08 | — | 0.24 | 0.27 | 0.41 |
| *Sphagnum* | 0.08 | 0.07 | — | 0.08 | 0.08 | 0.07 | 0.57 |
| *Filices* | 1.71 | 1.33 | 0.75 | 1.09 | 0.82 | 1.87 | 2.87 |
| *Dryopteris Linnaeana*-type | — | — | — | — | — | — | 0.08 |
| *Osmunda* | 0.16 | 0.22 | 0.17 | — | 0.16 | 0.20 | 0.24 |
| Unknown spores | 0.16 | 0.15 | — | — | — | 0.40 | 0.33 |

a mean size of 50.38μ ($\sigma$=4.03μ) for white pine (9 collections) and 46.00μ ($\sigma$=2.85μ) for red pine (10 collections). The size distribution of the maximum internal diameter of pine pollen in sample #6 (Fig. 5) has 2 modes, 37.0μ and 42.0μ. As in birch, the absolute size is smaller than that observed for modern pollen. The distribution shows, however, that bimodal size-frequency distributions can occur in mixed populations of pollen from white and red pine. Bimodal size frequency distributions of pine pollen in fossil material are often interpreted to indicate the presence of the pollen of jack pine (*Pinus banksiana*), which has a mean size of 45.9μ (Cain and Cain 1948). However, it is clear from these data that both red and jack pine, as Cain and Cain's measurements have already indicated, must be considered in the interpertation of bimodal distributions of fossil pine pollen.

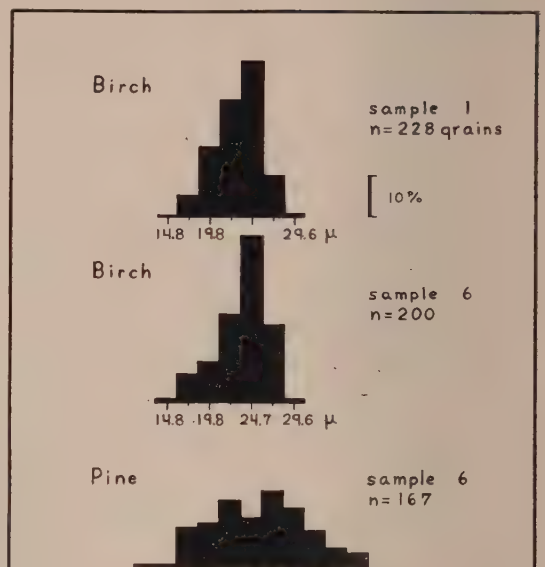


FIG. 5. Size distributions of birch, pine and spruce pollen in sediment samples.

The maximum internal diameter of spruce pollen in sample #6 was also measured (Fig. 5). Size measurements of pollen, treated with KOH and acetolyzed, are available for the 3 species that occur in the Memphremagog quadrangle. The mean pollen size for white spruce (5 collections) is 80.36μ ($\sigma$=5.45μ), red spruce (8 collections) 76.59μ ($\sigma$=4.73μ), and black spruce (3 collections) 62.17μ ($\sigma$=4.28μ) (Cain 1948; S. A. Cain and S. T. Andersen, personal communication). The size distribution of spruce pollen in sample #6 is bimodal, with modes at about 54μ and 67μ. Although the absolute size of the pollen is smaller than in modern pollen preparations it is likely that the mode at 67μ represents white and red spruce pollen, and the mode at 54μ, black spruce pollen. The bimodality of the distribution was unexpected because of the low frequency of black spruce in the forest (6% of the basal area recorded for spruce in the sample plots). However, spruce pollen in samples #5 and #7, measured several months later, displayed unimodal size distributions, skewed to the larger size classes. Bimodality in sample #6 may be the result of

statistical error or of an unusually large proportion of black spruce pollen in that sample. Although the data seem to indicate that black spruce is better represented in the sediments than the other spruce species, surface samples from Quebec (Potzger *et al.* 1956) indicate the reverse. The possibility that the spruce species differ in pollen production should be investigated, because changes in the percentages of fossil spruce pollen in pollen zone A in Massachusetts have been correlated with changes in the modal pollen size (Davis 1958). If the spruce species vary greatly in pollen dissemination efficiency, the changes in pollen frequency may have resulted from a change in the relative abundance of the species, rather than from a change in the absolute abundance of the genus in the vegetation.

## Comparison of the Pollen Frequencies and the Present Vegetation

Results of the forest survey and the pollen analyses are summarized in Figure 3 and Tables I, II and III. Two outstanding facts emerge from a comparison of these data. First, although there are large local differences in the composition of the vegetation, the pollen content of sediments now forming in Brownington Pond shows only slight differences. Even the spectrum from Spectacle Pond, about 15 miles from Browning Pond, is similar. Second, the pollen composition of the sediments shows little relation to the composition of the vegetation. Nearly all the tree species observed in the present vegetation are represented in the sediments, but quantitative relations are almost completely lacking. For most species and genera the percentages of total tree and shrub pollen in the surface samples are strikingly different from the percentages of total basal area in the forest stands (Fig. 6). The forest survey indicates that the maples, arbor vitae, balsam fir, spruce, birch and poplar constitute about 75% of the forest stands. Although the sample is smaller than desirable in a region of such diverse vegetation, even casual observation of the forest would support this conclusion. In contrast to the forest survey, birch, beech, hemlock and pine are the most abundant pollen types in all the samples.

To use our data to estimate relative efficiencies of pollen dissemination, we must assume that most of the pollen deposited at Brownington Pond had its source within the Memphremagog quadrangle. This cannot be proved on the basis of the pollen spectra because much of northern New England and southern Canada has a similar flora, at least

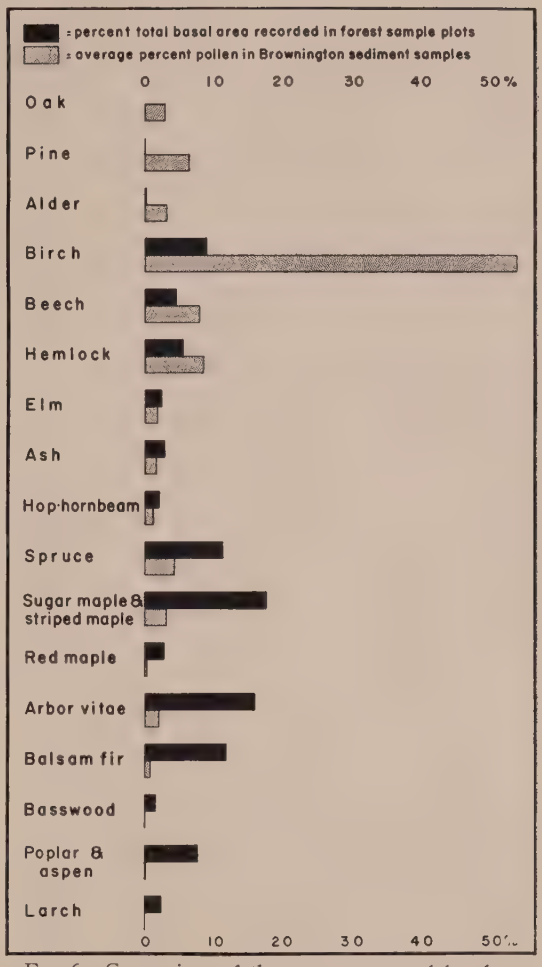


Fig. 6. Comparison of the percentage total basal area recorded in sample plots and the average pollen percentage in sediments from Brownington Pond of seventeen species and genera.

on the generic level. However, in regions of widely divergent vegetation, series of surface peat and humus samples indicate that in forested regions the majority of the pollen is contributed by trees within a few miles of the sampling station (Tsukada 1958). In partially forested or non-forested regions the frequency of tree pollen transported from a "long distance" is much higher. For example, in Norway the frequency of "long-distance" tree pollen as opposed to "local" tree pollen is thought to be roughly the same as the frequency of non-arboreal pollen (Faegri and Iversen 1950). This generalization has not yet been tested in eastern North America, but if it is true we may expect that 80-90% of the tree pollen at Brownington Pond is from "local" trees, and 10-20% has been transported from trees growing at a "distance." Unfortunately the area

regarded as "local" cannot be easily defined and depends upon the relative buoyancy of each pollen type. According to Faegri and Iversen (1950) pollen is only occasionally transported hundreds of miles. They believe that the natural limit of pollen transport is 50-100 km (30-60 miles) and that the great majority of pollen falls to the ground long before it has traveled that distance.

Considering the uncertainty of the origin of the pollen and the small size of the forest sample, it is not possible on the basis of our data to rank the trees according to their pollen dissemination efficiency. We can only provide a rough rank-order by observing those genera that are over-represented in the sediments (according to our data) and those that are underrepresented. It should be emphasized that these relations will not necessarily hold in other pollen spectra even though other variables are equal, because the pollen percentages are relative. For example, genera that are overrepresented here may be underrepresented in regions where genera with high pollen production are more abundant.

*Overrepresented pollen types.*—Oak pollen is highly overrepresented in the sediments. The frequencies are similar in all samples, suggesting that oak pollen is readily dispersed by wind. Although European species have generally been considered moderate to poor pollen producers, several authors have noted that the pollen is readily transported by air currents (Hesmer 1933; Vareschi 1935; Dyakowska 1936). Similar observations have been made in Japan (Tsukada 1958). Potzger *et al.* (1956) found oak pollen in surface samples in Quebec that were collected at least 5 miles from the nearest stands of oak, and Carroll (1943) observed oak pollen in moss polsters collected in the Great Smokies at an elevation 1,950 ft higher than the nearest oak trees. The relatively high frequencies of oak pollen in samples from the Memphremagog quadrangle, where oak trees are extremely infrequent, suggest that red oak in this region is a heavy pollen producer. Another possibility is that the high frequencies are due to long-distance transport, but oak is infrequent in a wide area surrounding the quadrangle (Fig. 4). The characteristics of pollen dissemination in other species of oak, and in red oak in other parts of its range, should be studied further.

Pine is also overrepresented. The percentage is highest in sample #10, as was expected since red and white pine are common along the shore of Spectacle Pond. However, it is surprising that there is so little difference in the pine pollen percentages at this site and at Brownington Pond, where pine is infrequent. Pollen produced by the few pine in the area apparently is readily dispersed and falls in an even rain over a wide area. Dyakowska (1936) has shown that pine pollen is buoyant in air, and surface sample studies have shown that it is transported over long distances (Hesmer 1933; Vareschi 1935; Lüdi 1937; Carroll 1943; Aario 1944; Potzger *et al.* 1956). The high frequencies of pine pollen in comparison to the low frequency of pine in the forest probably indicate that red and white pine, like European pine species (Pohl 1937), produce pollen in great quantity.

Birch and alder are also highly overrepresented, although the differences in per cent basal area and per cent pollen are not so striking as in pine and oak. Potzger *et al.* (1956) found in Quebec that birch was overrepresented in pollen spectra somewhat similar to ours.

*Proportionately represented pollen types.*—Pollen percentages of hemlock and beech slightly exceed the per cent basal area recorded for these species, and the pollen percentages of ash, elm, spruce and hop-hornbeam are equal to or slightly less than their per cent basal area. Within the limits of accuracy of this study, all these genera or species are about the same in their representation in the pollen spectra as compared to their representation in the forest.

*Underrepresented pollen types.*—The percentages of maple, arbor vitae, fir, poplar, larch and basswood pollen all are much lower than the per cent basal area recorded in the forest. Similar results have been obtained by Potzger *et al.* (1956) in Quebec, where arbor vitae, larch and mountain maple were found to be poorly represented in surface pollen spectra. They also found that although the basal area per acre of balsam fir and spruce (mostly black spruce) was approximately equal, the ratio of fir to spruce pollen was 2:3. In the Memphremagog quadrangle the basal area of balsam fir and spruce (mostly red and white spruce) is again approximately equal; the ratio of fir to spruce pollen at Brownington Pond is in most cases about 1:4. Balsam fir appears consistently less well represented in pollen samples than spruce, regardless of which spruce species are considered. Fir species may differ in pollen production, however. In an area in the Great Smokies where the basal area of Fraser's fir (*Abies Fraseri*) was two thirds as great as spruce (red spruce), the pollen frequencies of fir and spruce were approximately equal (Carroll 1943).

The percentages of arbor vitae pollen are low (4.5% maximum) and vary from one sample

to another. Arbor vitae is abundant in forests near the shore, yet pollen percentages are lower in sample #10 and in the shallow water samples from Brownington Pond than they are in samples from deeper water. Possibly arbor vitae pollen is less resistant to decay than other pollen types (Hesmer 1933). As the mud surface beneath shallow water is occasionally exposed to oxidative conditions that promote pollen degradation, the frequencies of arbor vitae pollen in shallow water samples may be reduced, relative to other pollen types, by decay under oxidative conditions.

*Other tree and shrub pollen types.*—Pollen of butternut, hickory and chestnut was found in low frequencies in most surface samples, although these genera were not observed in the sample plots. A few butternut trees were observed along roadsides, but hickory and chestnut were not seen in the quadrangle and are either infrequent or absent. The efficiency of pollen dissemination in these species should be tested in areas where they occur in greater abundance.

Rosaceous trees, willow, black alder, hazel, *Viburnum, Ericaceae, Myricaceae* and poison sumac occurred in low frequencies in the sample plots or were found as pollen in the sediments. The frequencies are too low to allow an estimate of their relative representation in the pollen spectra.

*Non-arboreal pollen types.*—It is estimated that 45% of the Memphremagog quadrangle is non-forested. Most of the non-forested land is used as pasture, and supports a rich growth of sedges and grasses. Weeds are common along roadsides and in meadows. The herbaceous flora, however, is poorly represented as pollen in the sediments. Percentages vary from 6% of total pollen in samples taken near the shore of Brownington Pond, to 16% in sample #6 from the center of the lake. Very little herbaceous pollen, apparently, comes from the aquatic vegetation near the shore. The pollen of shallow water rushes and sedges in Brownington Pond either is produced in minute quantities or its proportion in the sediments is reduced by tree pollen. The variations in non-arboreal pollen percentages from one sample to another are in contrast to the uniformity of the tree pollen percentages. There are several possible explanations: 1) During collection, sample #6, which was collected with a Livingstone borer, could have been mixed with older sediment with a high NAP (non-arboreal pollen) frequency. However, the mud underlying sample #6 has been analyzed and found to have the same or lower NAP frequency, and statistical tests indicate that mixing was not complete. 2) The frequency of NAP may have been reduced by differential degradation, as has been suggested in the case of arbor vitae. Lüdi (1937) has suggested that non-arboreal pollen is less resistant to decay than arboreal pollen. However, this explanation is not satisfactory because sample #10, in which the pollen was in noticeably poor condition, has a higher NAP frequency (13.6% herbs, 9.4% shrubs) than any of the samples from Brownington Pond. 3) The proportion of NAP in sediments near the shore has been reduced by pollen from nearby trees. This assumption fails to explain the high NAP percentages in the sample taken near the shore of Spectacle Pond. 4) The patchy distribution of forests may affect the dispersal of non-arboreal pollen, because herbaceous pollen is shed near the ground and dispersed by local air movements (Hesmer 1933)[3]. The waters near the shore of Brownington Pond may be protected by nearby forests from the local winds that carry NAP. The effect of a forest near the shore may be similar to the vertical screening effect produced by forest canopies (Dengler 1955; Potzger *et al.* 1956). In contrast, Spectacle Pond is relatively unprotected because it is bordered on one side by a meadow. Possibly the pollen deposited at an exposed site such as the center of a large lake is derived from a larger area than pollen deposited at sites protected from wind by nearby forest.

## Significance of Study for Interpretation of Fossil Pollen Diagrams

In the comparison of the present vegetation of the Memphremagog quadrangle with the pollen in surface samples, little quantitative relation was found between the frequencies of pollen types and the frequencies of species in the vegetation. The complexion of past vegetation cannot be deduced accurately from fossil pollen spectra before the relations between the present pollen rain and the present vegetation are better understood. An understanding of these relations depends upon greater knowledge of at least four variables: 1) differences in amounts of pollen produced by different species, which may themselves show genetic, environmental and ontogenetic variations; 2) differences in pollen transport distances, which vary widely because of the physical properties of the pollen grains themselves, and are influenced by topography, vegetation cover, and atmospheric conditions that differ from year to year; 3) differ-

[3] Rowley (1955), however, found similar numbers of grass pollen in pollen traps located about 800 ft apart, one in a meadow, the other on the forest floor.

ences in preservation and patterns of deposition of pollen types, which may be affected both by the properties of the different kinds of pollen as well as by the characteristics of the collecting basins; and 4) local variations in species distribution and frequency of the present vegeation. Unfortunately, this study can make little contribution to solution of these problems, and can only emphasize their existence.

Furthermore, large local variations in the forests of the Memphremagog region produce essentially uniform pollen spectra in the lake sediments. This uniformity suggests that estimates of the local variations of past vegetation probably cannot be made on the basis of pollen diagrams. The pollen diagrams will record the contribution of each species that grew in the region from which the pollen came, rather than the contribution of presumed plant communities. Species with quite different ecological requirements will occur together in pollen spectra if the region contributing pollen is large.

Climatic interpretations of pollen diagrams are based on the presence or absence of "indicator species" and on changes in pollen frequencies. The presence or absence of pollen has little meaning, however, unless pollen dispersal characteristics are known. Similarly, interpretation of changes in pollen frequencies depends on knowledge of the size of the region that contributes pollen. The pollen deposited in Brownington Pond, for example, may have come from trees within a 5 or a 50 mile radius. Changes of pollen frequency in the sediments of the lake may thus represent changes in the vegetation of an area ranging in size from 75-7500 sq miles. Interpretations of such changes will remain entirely speculative until the meanings of the terms "regional vegetation" and "regional pollen rain" are clarified by many comparative studies of the present vegetation and the present pollen rain in North America.

The complexity of the American flora adds difficulties to the solution of the problems we have outlined. Much of the data in the literature cannot be applied to North America because congeneric species vary in pollen production and pollen bouyancy. Even American estimates of pollen production, if they are based on one species or a mixed population of species, cannot be applied to generic pollen types. If species within a genus show extreme variation in pollen production, it will be difficult or impossible to interpret changes in frequency of fossil pollen types unless species identifications are made.

It is our hope that this study will prompt further research into the basic principles of pollen analysis. Clarification of problems outlined here will make future analyses of fossil pollen deposits more meaningful, and will increase the value of previous work.

## Summary

The vegetation of the Memphremagog quadrangle in northern Vermont has been surveyed in some detail. Quantitative studies of 18 sample plots in the vicinity of Brownington Pond indicate a highly diverse forest vegetation. Pollen was analyzed in samples of the mud bottom of Brownington Pond and of Spectacle Pond, 15.5 miles distant. The tree pollen percentages in all the samples were closely similar, indicating that the tree pollen rain in the region is fairly uniform. Variations in NAP percentages may indicate that the non-arboreal pollen rain is not uniform because it is distributed by local air currents. Pollen frequencies of tree species show little quantitative relation to the basal area percentages recorded in the forest sample plots. On the basis of comparison of the basal area percentages in the sample plots and the percentage pollen in the sediment samples, the more common tree and shrub species of the region have been divided into 3 groups according to relative representation in the pollen sum. In order of decreasing representation, the groups are: 1) red oak, pine (2 spp.), alder and birch (3 spp.); 2) beech, hemlock, elm, spruce (3 spp.), ash (2 spp.) and hop-hornbeam; and 3) maple (4 spp.), arbor vitae, balsam fir, poplar (3 spp.), larch and basswood.

Size measurements were made of the pollen of birch, pine and spruce and compared to the mean size of pollen of the species that now occur in the region. The size-frequency distribution of yellow, white and gray birch pollen was unimodal and skewed to the larger size classes, and the distributions of both red and white pine pollen and white, red and black spruce pollen were bimodal.

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# OBSERVATIONS ON THE EFFECT OF A BURN ON A POPULATION OF *SCELOPORUS OCCIDENTALIS*[1]

## Introduction

A common inhabitant of the chaparral areas of Southern California is the Western Fence Lizard, *Sceloporus occidentalis longipes*. The purpose of this field study was to learn as much as possible about the effect of a burn on a population of these lizards.

The study was conducted in the San Bernardino Mountains, near the City of San Bernardino, San Bernardino County, California. In September of 1956, a serious fire swept this area and, in a particular location along Highway 30, about 2 miles below the City Creek Ranger Station, the fire was abruptly halted, leaving a sharp line of demarcation between the burned and unburned portions (Figure 1). This situation made for an excellent location in which to conduct the field study.

The study area was approximately 100 yards long by 60 yards wide and was at an altitude of 2650 feet. It was a typical chaparral community with Yerba Santa (*Eriodictyon angustifolium*) and Mohave Buckbrush (*Ceanothus perplexans*) predominating, which placed the area in the Upper Sonoran Life Zone (Hall and Grinnell 1919).

## Methods

Beginning in early February 1957, the study area was visited at regular intervals and the lizards were noosed or captured by hand. As the weather warmed, however, the lizards became increasingly active, making the noose the only practical method of capturing them alive.

As each specimen was taken, the date of capture was noted, it was identified, sexed, measured (snout-vent length) and its toes were clipped in various combinations, thus rendering it permanently recognizable. The toes were identified as follows: starting with the right front foot, with the limb facing anteriorly, the outside toe was designated as "A" and the other toes were lettered consecutively, from right to left, with the limbs in a similar position. In order to interfere as little as possible with normal activity, no more than 2 toes were clipped from each lizard and no more than one toe was clipped from each foot.

The specimen was then painted on the back, just anterior to the hind limbs, according to the following color code: Red, if taken in the burned area and Yellow, if taken in the unburned portions. This accomplished, the animal was released at the point of capture. The coloring, of course, made it possible to observe lizard movement without resorting to capture.

## Results

A section 2 miles north of the project location and at least 2 miles from any unburned portion, was checked in early February and several specimens of *Sceloporus occidentalis longipes* were taken from under rocks. The lizards were dormant and covered with ash but were otherwise in good condition. Lizards, in a similar situation and condition, were also taken in the project location.

In the gross observations of the lizard movements, no groups of lizards were seen moving between burned and unburned areas. No mating attempts were noted and a few fights were seen but they were of short duration.

Fig. 1. A view of the line of demarcation between the burned and unburned zones.

In the burned area, 34 lizards were tagged and released. Subsequently, 13 of them were recaptured (38% return) and they were taken in the same area with the exception of one which had moved into the unburned area.

Out of a total of 22 lizards which were marked and released in the unburned area, 6 were recaptured (17% return). Of the 6 retaken, 4 had remained in the unburned portion and two had moved into the burned area.

In June, 1957, 24 lizards were shot, 7 of which had been marked, and their stomach contents were examined. Insects of the order Lepidoptera seemed to be an important part of the diet in both burned and unburned areas. Coleoptera were also well represented in both portions. Hemiptera were in greater abundance in the burned area. Hymenoptera and Orthoptera were represented in the sample but only in small quantities.

Most of the female lizards from both areas, contained eggs which were apparently ready to be deposited.

No young lizards were observed or taken in the burned area.

[1] Derived from a Master's Thesis submitted to Long Beach State College, Long Beach, California.

## Conclusions

The soil, ½ inch below the surface, does not ordinarily rise above 60°C during a chaparral fire (Sweeney 1956). Therefore, it was not surprising that the lizards were able to survive the blaze, merely by retreating into their burrows or seeking shelter under rocks.

There was no definite movement of lizards from burned into unburned areas. In the reverse direction, it appeared that there was some movement. However, this conclusion is based on the 2 lizards which were captured in the burned area, having moved from the unburned area. It is, however, logical that the movement is in this direction. Since the Western Fence Lizard prefers rocky areas (Stebbins 1954), it suffers no disadvantage from the loss of ground cover and, in addition, because young lizards tend to seek inadequate shelter (Fitch 1940), they would probably not survive as well as the adults in better insulated situations and this would lessen the population pressure in the burned areas.

The burn evidently had little effect on the food preferences of the lizards. The diet in the burned and unburned areas was essentially the same. The insects apparently thrive well in a burned area, thus providing a good food supply for the lizards.

Reproductive activities seemed not to have been seriously affected by the burn since the females in both areas were ready to deposit eggs.

## Summary

(1) *Sceloporus occidentalis longipes* is able to survive a burn evidently protected by the insulating qualities of the soil.

(2) Young lizards are more vulnerable to a blaze because they seek inadequate shelter. This lessened population pressure may encourage movement into the burned area from the unburned parts.

(3) The burn seems to have had little effect on the diet of the lizards. The type of food ingested by lizards in the burned and unburned areas, is essentially the same.

(4) Reproductive activities were not affected as females in both areas were ready to deposit eggs in early June.

## Acknowledgment

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# A CAGE FOR THE STUDY OF GROWTH IN SEA URCHINS

In connection with studies of the growth rate and longevity of the common green sea urchin *Strongylocentrotus droebachiensis* (O.F. Müller) on the coast of northern New England, cages containing urchins have been submerged in the ocean for periods up to a full year. This work has been supported by the National Science Foundation (N.S.F. G-4959). Several types of cages have been tried, but the one described below has proved the most satisfactory. For advice concerning its design, appreciation is expressed to Dr. G. M. Moore of the Department of Zoology at the University of New Hampshire.

The appearance and construction of the cage are shown in Figure 1. The wood used is one-inch planed red oak, and all metal parts are galvinized except for brass pins in the hinges and hasp and the soft iron rivets used for joining the wooden pieces of the cover. The wire screening, which is much heavier, stronger, and more durable than the usual hardware cloth, is designated in the trade as "2 mesh .063 galvanized after woven wire cloth", and locally roofers call it "picker screen."

The more important wooden pieces used in the construction of the cage are shown in Figure 2. If one does not anticipate study of animals smaller than would be retained by the wire of the cage, one may omit the cross pieces with the 3½" holes. These are for the insertion of tapered one-pint polyethylene containers with snap-on covers. If the plastic containers are used, several holes

Fig. 1. Front and side view of sea urchin cage (Photograph by University of New Hampshire Photographic Service).

as large as possible but small enough to keep the animals in should be made in both covers and bottoms to allow for circulation of water.

For the performance of growth experiments involving

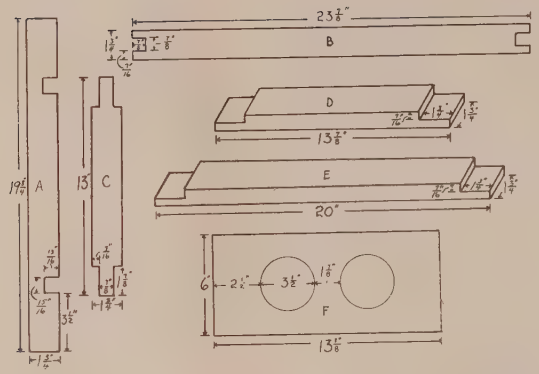


FIG. 2. Wooden parts used in the construction of sea urchin cage. A. End pieces, horizontal (4), B. Long pieces, horizontal (4), C. Vertical end pieces (4), D. Cross pieces of cover (2), E. Long pieces of cover (2), and F. Inside supports for plastic boxes (2).

the use of these cages, the choice of location is of the utmost importance. Preferably this location should be favorable to the species being studied, not heavily frequented by inquisitive people, and protected from the direct surf. In such a location these cages have been weighted down with rocks, tied together in sets of 3 and then tied to larger rocks. After a year the wood showed some evidence of attack by *Limnoria*, and the wire was beginning to rust. Even so, it appeared that they could safely have been used for several more months.

In any studies using such cages it is essential to give careful attention to feeding the animals, to removing decomposing food and dying animals, and to keeping the mesh of the cages free of any debris that might impede the free circulation of the water.

It appears likely that cages of this general type should be useful in studies involving other aquatic animals, and it is hoped that their use may result in the accumulation of additional data relevant to the growth rate and longevity of the species studied.

SUMMARY

The construction of a cage for holding sea urchins and other marine animals during growth experiments has been described. In view of the small amount of available data pertaining to the growth rates of the vast majority of marine invertebrates, the usefulness of data obtainable from caged specimens is discussed.

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* In regions of severe shipworm infestation, cages with galvanized iron frames are advisable.

## BEES, DAPHNIA, AND POLARIZED LIGHT

### INTRODUCTION

Although a variety of animals, mostly arthropods, have been shown to orient to the polarization plane of polarized light, the means of orientation has been the subject of considerable speculation. Optical and physiological analyses of the visual apparatus by a number of authors have until recently revealed no clear and convincing evidence of a device by which the polarization plane is detected.

This note presents a set of simple experiments that will distinguish which of 3 possible kinds of polarization analyzers is employed by an animal orienting to the polarization plane of overhead light. The 3 kinds of analyzers are characterized by their location and operating principles.

The first of these analyzers is not only extra-ocular but is entirely extra-animal. Polarized light may produce patterns of reflectance and scatter from the substratum and similar patterns of scatter from surrounding water, in which the bright and dark areas can be predicted from Fresnel's equations and from scattering theory (for a lucid discussion of these and other properties of polarized light, including the effect of half-wave plates described below, see Jenkins and White 1958). The intensity variations in these patterns have been shown to be adequate for brightness discrimination and therefore for phototactic responses in arthropods (Baylor and Smith 1953 and in press, Bainbridge and Waterman 1959). Thus photopositive animals restrained from vertical movement may move toward the brighter areas of these patterns, which lie in the axis perpendicular to the polarization plane. Discrimination of the polarization plane in overhead light through the use of such brightness patterns will in this paper be called extra-ocular polarization analysis.

The 2nd kind of analyzer is intra-ocular and depends on one or more reflections or refractions from lenticular surfaces in the dioptric apparatus as predicted by Fresnel equations. These phenomena may occur in ommatidia with optic axes at a considerable angle to the incident light beams. By various combinations of refraction, reflection, and even scatter in the lenses, a small amount of this off-axis incident light may actually reach the rhabdomeres, where it may be seen as "glare" if the projected visual field of the ommatidia involved is very dark compared with the brightness of the primary light source. The brightness of such glare will vary with the azimuth angle of the ommatidium to the polarization plane, and orientation becomes possible if the animal is able to discriminate such brightness variations. If the glare is primarily refracted to the rhabdomeres its brightness is greatest in ommatidia with optic axes parallel to the polarization plane, least in those perpendicular to the plane. If the glare, following initial refraction, is primarily reflected or scattered internally in the dioptric apparatus to the rhabdomeres, then its brightness is greatest in ommatidia with axes perpendicular to the polarization plane, least in those parallel. This means of polarization discrimination will be called intra-ocular reflection-refraction analysis.

The 3rd way of discriminating the polarization plane requires that the animal detect the plane with those ommatidia looking directly at the light source, much as man can do by rotating a sheet of polaroid. The radial array of rhabdomeres in each ommatidium is presumed to act like a radial or concentric polaroid. The rhab-

domeres are presumed to be dichroic with parallel fast axes for opposite pairs of the array. This or any equivalent means of discrimination will be called intra-ocular dichroic analysis.

## Experiments

It is possible to infer from the data of a series of behavior experiments which kind of polarization analyzer is employed by the experimental animal. These experiments are conducted in a darkroom on a horizontal arena beneath a vertical parallel or slightly divergent beam of polarized light. In the basic experiment the arena has a black floor and black, shaded sides so that the animal sees the light overhead, the floor beneath, and very little else. All postulated means by which orientation can occur will operate in this experiment, provided of course that the cooperation of the animal can be secured.

Orientation can be measured by inscribing in the arena 2 sets of parallel lines, one parallel with the polarization plane and one perpendicular to it. In our experiments the lines were one inch apart and formed an 8-inch square, with at least an inch of unlined arena at the edges. As the animal moves, one observer counts the lines crossed in one set, while a second observer counts lines crossed in the other set. A measure of the degree of orientation is given by the percentage of one of these counts in the sum of the 2. The percentage of path vector perpendicular to the polarization plane is given below.

The arena for bees was 10 inches square and ¼ inch deep, with the lines inscribed on a thin, clean glass cover. The black floor was a dull paper with a slight grain having a reflectance bias. To allow correction for this bias the polaroid was used in 2 positions, parallel and perpendicular to the grain. Light intensity at the arena was about 12 foot candles, and the temperature varied from 22° to 25°C. Six bees (Table I) averaged 63% orientation. The result for each bee is the sum of several trials for each position of the polaroid, and it is obvious from a study of the trial data (Baylor and Smith, in press) that real differences exist between bees; some orient more than others in a given situation.

Table I. Bees on dull black paper. Plane of polarization in overhead light is either left-right (A) or front-rear (B) with respect to the observers. Numbers are lines crossed by each bee during several 2-minute runs and represent inches of path vector left-right (a) and front-rear (b). Percentages are of those portions of the paths that are perpendicular to the polarization plane.

| Bee | Polaroid Position A | | | Polaroid Position B | | | Average |
|---|---|---|---|---|---|---|---|
| | a | b | % | a | b | % | % |
| A | 131 | 241 | 64.8 | 317 | 226 | 58.4 | 61.6 |
| B | 129 | 255 | 66.4 | 225 | 159 | 58.6 | 62.5 |
| C | 170 | 247 | 59.3 | 216 | 162 | 56.5 | 57.9 |
| D | 151 | 341 | 69.3 | 225 | 149 | 60.2 | 64.7 |
| E | 164 | 302 | 64.8 | 337 | 203 | 62.4 | 63.6 |
| F | 99 | 254 | 72.0 | 246 | 170 | 59.2 | 65.6 |
| Ave. | | | 66.1 | | | 59.2 | 62.7 |
| Std. Dev. | | | 4.4 | | | 2.0 | 2.5 |

If a dull white arena floor is used, extra-ocular analysis becomes impossible, since dull white surfaces offer a nearly uniform field of brightness under polarized light. Intra-ocular reflection-refraction analysis will be impaired by the flood of depolarized reflectance from the floor, although a weak pattern may be discernible in ommatidia looking somewhat above horizontal. Intra-ocular dichroic analysis, on the other hand, is undisturbed; the overhead light remains as it was over a black floor.

Bees do not orient on white paper (Table II), behavior suggesting the absence of an intra-ocular dichroic analyzer in these organisms.

Table II. Bees on white paper or clean mirror. Percentages as in Table I. The relative orientation is the ratio of the present orientation, minus 50%, divided by the black paper orientation of the same bee on Table I, minus 50%. For bees G through J the ratio denominator was taken as 12.7, the average from Table I.

| Bee | White Paper % | Relative Orientation | Clean Mirror % | Relative Orientation |
|---|---|---|---|---|
| A | 52.5 | 0.216 | 53.2 | 0.275 |
| B | 49.9 | −0.008 | 53.6 | 0.288 |
| C | 43.2 | −0.860 | 55.0 | 0.633 |
| D | — | — | 51.7 | 0.116 |
| E | — | — | 54.2 | 0.309 |
| F | — | — | 57.5 | 0.482 |
| G | 51.8 | 0.142 | — | — |
| H | 45.8 | −0.331 | — | — |
| I | 52.4 | 0.189 | — | — |
| J | 53.7 | 0.291 | — | — |
| Ave. | 49.9 | −0.052 | 54.2 | 0.351 |
| Std. Dev. | 3.9 | 0.412 | 1.9 | 0.181 |

If a clean, front-surface mirror is used instead of a black floor, extra-ocular analysis becomes more difficult. Oblique reflectance to the animal from the peripheral regions of the arena (where the brightness pattern is strongest) is very much less from a mirror than from black paper. Even more important, however, is that its brightness variations are also less. Baylor and Smith (in press) found brightness variations to be only ⅓ as great from a mirror as from black paper, even when expressed in relative terms. On the other hand, the downward and upward directed illumination, fully polarized, vertical, and with a brightness that is independent of the position of the polarization plane, remains ideal for either kind of intra-ocular analysis.

Bees orient only 35% as well on a mirror as on black paper (Table II). Since this follows closely the weakening of pattern in extra-ocular reflectance, the existence of only an extra-ocular analyzer is suggested.

A more critical test making the same discrimination is based on the effect of half-wave plates. The orientation of an animal on a black surface is first measured, and then a large half-wave plate is inserted just below the polaroid. This rotates the polarization plane 90° more or less (depending upon wavelength), and the new orientation of the animal is measured. The difference between the 2 orientations is the effect of the large plate. Then the large plate is removed, and a small plate on the end of a thin wire is carefully held over the animal as it moves. This alters the light falling on the animal, but not the light falling on most of the environment. The effect of the small plate on orientation can be compared with the effect of the large plate to determine the relative

roles of illumination falling directly on the animal and that falling elsewhere on the arena.

A bee selected for very good orientation on black paper (Table III) showed a considerable effect from the large plate, but no significant effect from the small, one-inch square plate. Hence, all of the orientation observed must be ascribed to an extra-ocular analyzer, with the bee responding in a simple way to a brightness pattern in its environment. Although the wave plates were not good (two layers of "Scotch tape"), their imperfection is accommodated in the measures, and the power of this test is very high.

TABLE III. Effect of half-wave plates on a bee selected for good orientation. The relative effect of the small plate is the ratio of the effect of the small plate to the effect of the large wave plate. The standard error of the relative effect was computed 2 ways: as a function of the other errors listed, giving 0.066, and from 5 estimates of the relative effect using each small plate trial and the nearest trials in time for no plate and for the large plate, giving 0.074.

| Condition: | No. trials | Ave. % | Std. Error | Effect |
|---|---|---|---|---|
| No wave plate (control) | 12 | 68.1 | 1.04 | |
| Small wave plate | 5 | 66.75 | 0.87 | 1.35 |
| Large wave plate | 8 | 47.9 | 0.41 | 20.2 |
| Relative effect of small wave plate: | | | | 0.067 |
| Standard Error: | | | | 0.070 |

With aquatic animals the experiments are similar. *Daphnia magna* were run in a glass dish 12 inches in diameter and 3 inches deep, using 1½ inches of clarified water. The 2 sets of lines were inscribed on the floor of the dish. An arena floor of beeswax impregnated with carbon black was poured so as to be grainless, and was found to be an excellent dark surface for brightness patterns under polarized light. Black cloth surrounded the dish, whose sides were completely shaded from the light. Daphnids orient very well (Table IV). Although the precentages are much higher than for bees, this is largely a result of the small size of daphnids, which are much less likely than bees to cross lines while turning around.

TABLE IV. Daphnids on black wax or clean mirror surfaces. Percentages and relative orientations as in Tables I and II. Three daphnids used.

| Daphnid | Black wax % | Clean mirror % | Relative orientation using mirror |
|---|---|---|---|
| Small | 92.2 | 94.7 | 1.06 |
| Medium | 92.5 | 80.7 | 0.72 |
| Large | 86.1 | 88.2 | 1.06 |
| Ave. | 90.3 | 87.9 | 0.95 |
| Std. Dev. | 3.6 | 7.0 | 0.20 |

Using a white paper floor (Table V), 84% of the orientation persists. This does not necessarily imply the presence of an intra-ocular analyzer, however, since an additional extra-ocular cue is present: scatter in the water. This cue cannot be removed, but it can be made less visible by using a white periphery. Using unshaded white paper around the dish and a black floor, 43% of the orientation persists. When both the periphery and floor are white, and average of 13% of the original orientation remains (Table V) with a considerable variance and no significant differences from zero even at the 0.5 level. It seems reasonable to conclude that the orientation can be eliminated completely if the surroundings of the animal are suitably whitened, even though the overhead polarized light remains in full view, and that an intra-ocular dichroic analyzer is not involved in the orientation of daphnids.

TABLE V. Daphnids on several white backgrounds. The relative orientation compares present orientation, minus 50%, with that on black wax, minus 50%, given in Table IV.

| Daphnid | White floor % | Rel. Orient. | White sides % | Rel. Orient. | Both white % | Rel. Orient. |
|---|---|---|---|---|---|---|
| Small | 87.0 | 0.88 | 53.0 | 0.07 | 69.0 | 0.45 |
| Medium | 85.5 | 0.84 | 87.0 | 0.87 | 39.5 | −0.25 |
| Large | 78.5 | 0.79 | 63.0 | 0.36 | 56.5 | 0.18 |
| Ave. | 83.7 | 0.84 | 68.0 | 0.43 | 55.0 | 0.13 |
| Std. Dev. | 4.5 | 0.045 | 17.0 | 0.41 | 15.0 | 0.35 |

Using a clean mirror floor (Table IV) orientation is as good as on black paper. This experiment, however, is not as critical for an aquatic animal as for a terrestrial one. The brightness of scatter in the water is about doubled and this may compensate for the decrease in signal from the floor.

The wave plate experiment remains critical. For daphnids, good mica half-wave plates were obtained, and the large plate inserted beneath the polaroid caused a nearly complete reversal of orientation (Table VI).

TABLE VI. Effect of half-wave plates on daphnids, using a black wax surface. Relative effect compares the effect of the small wave plate to that of the large wave plate, using data of Table IV for orientation with no wave plate.

| Daphnid | Small wave plate % | Large wave plate % | Relative effect of small plate |
|---|---|---|---|
| Small | 63.5 | 37.6 | 0.53 |
| Medium | 62.6 | 7.4 | 0.35 |
| Large | 57.3 | 43.0 | 0.67 |
| Ave. | 61.1 | 29.3 | 0.517 |
| Std. Dev. | 3.3 | 19.2 | 0.161 |

The small plate (which was a piece of the large one) also had a considerable effect, amounting to 52% of the effect of the large plate.

These experiments were repeated using a mirror floor. If both intra- and extra-ocular analyzers are involved to account for the partial effect of the small plate, the relative effect of the small plate using a mirror floor should be higher than using a black floor, since the intra-ocular signal is doubled, while, although the scatter signal is doubled, the floor reflectance signal is much reduced. Results were similar, except that the relative effect of the small wave plate was 68% (Table VI). Using a paired analysis and a one-tailed test, the difference from 52% is just significant at the 0.05 level.

### Discussion

Before drawing conclusions several possible artifacts must be examined. Possibly only an intra-ocular analyzer is involved, and the partial effect of the small plate is a result of imperfect alignment while it is held by hand over the animal. To test for the effect of such angular errors, the large plate was inserted 10 degrees out of alignment (with its fast axis 35°, rather than 45°, from the polarization plane). The relative effect, compared with the same plate correctly aligned, averaged 74% (Table VII). Since this amount of misalignment probably exceeds the maximum momentary deviation of the small plate, and is certainly much greater than the average error, the failure of the small wave plate to produce as great an effect as the large plate cannot be ascribed entirely to position errors.

Table VII. Effect of half-wave plates on daphnids, using a clean mirror surface. The first 3 columns are comparable to those of Table VI. The last 2 give only the relative effect of 2 possible artifacts, compared with the effect of the correctly aligned large plate.

| Daphnid | Small plate % | Large plate % | Rel. Effect | Rel. effect of Misaligned large | Rel. effect of Inactive small |
|---|---|---|---|---|---|
| Small..... | 50.0 | 25.8 | 0.650 | 0.737 | −0.06 |
| Medium.. | 40.0 | 15.6 | 0.627 | 0.657 | 0.00 |
| Large..... | 29.7 | 13.1 | 0.777 | 0.830 | 0.13 |
| Ave..... | 39.9 | 18.2 | 0.685 | 0.741 | 0.02 |
| Std. Dev.. | 10.2 | 6.7 | 0.081 | 0.087 | 0.06 |

A second possible artifact lies in the other direction: that in fact the small wave plate has no effect except as a disturbing moving object overhead. This is tested easily by holding the small wave plate over the daphnid in an inactive position (with its fast axis parallel or perpendicular to the polarization plane) so that the light is unaltered although the identical moving object is present. The results (Table VII) show no effect of disturbance.

Another possible explanation for the partial effect of the small wave plate is that the scatter pattern beneath the small plate in the water immediately around the animal is reversed and therefore tends to weaken the scatter pattern in the dish as a whole. The small plate used with daphnids was ¾ inches square, and the region of illuminated water was 10 inches square. Since the square of distance and area of source for the scatter compensate each other, the brightness pattern is reversed for a daphnid beneath the small plate in 3/40 of the total scatter signal, thus weakening the pattern by 6/40. This cannot possibly account for the average orientation over the mirror under the small wave plate, which was actually reversed so as to be 60.1% in the axis parallel to the polarization plane set by the polaroid. To account for this orientation the brightness pattern would have to be reversed in 25/40 of the total signal.

Thus, it can be concluded that daphnids orient through the combined action of an intra-ocular reflection-refraction analyzer and an extra-ocular analyzer, as earlier proposed by Baylor and Smith (1953, and in press), and recently supported by Waterman (1959). Details of the possible intra-ocular mechanism are given by Baylor and Smith (1957).

It can also be concluded that, at least in the experimental conditions used here, bees orient entirely by means of an extra-ocular analyzer. Whether this will be the case for bees in all situations remains to be varified. The naturally darkened surface of a brood comb has been shown to offer brightness patterns of reflectance with variations in intensity that are probably adequate for bees to use (Baylor and Smith, in press). In Stockhammer's (1956) bee-training experiments, the glass covered deep black floors, viewed necessarily at angles close to Brewster's angle by incoming bees, are ideal extra-ocular analyzers. In experiments where the sky is used, it should be remembered that the sky itself has a brightness pattern that probably can be discerned by bees. Such a pattern is a necessary concomitant to a polarization pattern. Wherever in nature a field of polarization is offered to an animal, a pattern of brightness will also be present. Occam's razor dictates that the latter must be eliminated before the former is invoked as an orientation cue.

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## A HOST-PARASITE INTERACTION CONDITIONED BY PREDATION

The steady densities of interacting populations of *Ephestia kühniella* (Zell.) and *Idechthis canescens* (Grav.) in a controlled environment can be markedly changed by manipulating the abundance of the egg-feeding mite *Melichares* (*Blattisocius*) *tineivorus* (Oud.).

In an ecosystem previously described (Flanders 1958), this conditioning of the *Ephestia-Idechthis* interaction by *M. tineivorus* was strikingly demonstrated. In this system the host and parasite populations are continuously self-perpetuating, apparently infinitely so, having been

in balance and free from any disease for over 3 years (28 host generations). The mite also has been continuously present. During about half of this period, however, the destructive action of the mite was neutralized by the miticide, Aramite. [*Melichares tineivorus* is likely to be present in any population of *Ephestia,* the adult mite being carried from place to place by the female moth. A single moth has been observed to transport 20 adult mites.]

When environmental conditions were highly favorable for the reproduction of the mite, over ⅓ of the *Ephestia* eggs was destroyed. The surviving *Ephestia* population nevertheless was twice that which occurred when conditions were much less favorable for the mite, and the destruction of moth eggs was at a minimum. The host-parasite interaction was conditioned by the numbers of moth eggs destroyed. This is in line with the arithmetically derived conclusion of Nicholson (1933) that, when a specific parasite and a specific host are interacting, a reduction of the power of increase of the host decreases the steady density of the parasite and increases the steady density of the host. The density of the host attaining the stage attacked by the parasite is decreased so that the parasite leaves unparasitized a larger fraction of the reduced host population.

It was found that the mite-caused mortality of *Ephestia* can be continuously maintained below the point at which it affects the host-parasite interaction. This is accomplished by the periodic application of an acetone solution of 5% Aramite to surfaces in the vicinity of host-infested grain.

In the system under consideration the acetone-Aramite solution was first applied on November 14, 1957. This was 16 months (12 host generations) after the ecosystem was initiated. The decline in the mite population was ascertained by sampling it once a day, the number of adult mites observable being noted during a one-minute inspection of the exposed areas. The monthly mite populations thus counted dropped from 240 in December to one in June. The consequent change in the host-parasite relation was first noted in April about 5 months after the first application of Aramite.

April 1 marked the end and beginning of the 2 distinctive phases of the host-parasite interaction. Each phase had a duration of approximately 13 months. The amount of food available to the host larvae was the same for each phase.

In the mite-affected phase, March 1957 to March 1958 inclusive, the production of host and parasite adults totalled 3,323; in the mite-unaffected phase, April 1958 to April 1959 inclusive, the production of such adults totalled 5,264.

The combined adult host and parasite populations during the first phase was regulated by the feeding of the mite on the host eggs, whereas that of the 2nd phase was regulated by the amount of wheat. The parasitization of the host larvae in the first phase was 53%, whereas in the 2nd phase it was 84%. Only in the 2nd phase was all the wheat consumed.

Actual counts of the total population show that during the mite-affected phase 1,756 host larvae became adult, whereas in the mite-unaffected phase only 883 did so; this, in spite of the fact that the total number of full-fed host larvae in the first phase was 3,323 and in the 2nd phase 5,264.

The greater larval population of the 2nd phase was accentuated by the precocious maturity of the parasitized larvae. With a given amount of food the host population, as measured by the number of cocoons, is greater when parasitization is high than when it is low. In the ecosystem here considered, the number of host cocoons derived from each weekly increment of 120 grains (Troy weight) of wheat ranged from about 60 in the first phase to about 90 in the 2nd phase. The average number of cocooned progeny per female host was 13 when parasitization was high and 10 when parasitization was low.

A noteworthy feature of the host-parasite interaction when parasitization is at a maximum, as in the mite-unaffected phase, and when such populations are totalled per month, is the marked periodicity and high amplitudes of the fluctuations in adult parasite populations. The peaks of parasite abundance then occurred at intervals of 3 to 4 months. There was little evidence of periodicity in the fluctuations of the adult host populations.

No periodicity was apparent in the adult population fluctuations of either the host or parasite in the mite-affected phase, but the amplitudes of the host fluctuations exceeded those of the mite-unaffected phase. It is noteworthy that under natural conditions the fluctuation of a host population having several natural enemies is least likely to be apparent (Smith 1929).

The larger fraction of parasitized host populations in the mite-unaffected phase is, in part, the effect of a situation peculiar to this particular system. As previously described (Flanders 1958), this ecosystem is provided with weekly allotments of grain, each allotment having a surface diameter of 43 mm and a depth of 14 mm. [The surface is not covered with vermiculite (Flanders 1959)]. During the mite-unaffected phase the action of the host larvae gradually reduces each allotment of grain to a depth of 6 mm. This material, when thus reduced, is largely if not entirely exhausted of nutriment, the weight of the residue (feces, etc.) being about 36 grains.

Since the habitats of the immature host populations are limited to these allotments of grain the gradual consumption of grain establishes a time gradient in the accessibility of the host which culminates when the entire infestation is within the areal range of the parasite. The complete gradation of accessibility requires about 3 months.

During the mite-affected phase this gradation is incomplete. A large portion of the wheat may be unconsumed (1/5 or more). This portion is limited to the top part of the mass of wheat, presumably an effect of the repellent action of the parasite's probing ovipositer and the lack of population pressure by the host larvae below, this population being relatively small because of the action of the egg-feeding mite. Consequently, a portion of the infested mass of material never comes within the areal range of the parasite, and a relatively high population of the hosts thus escape parasitization. During the mite-unaffected phase any repellent effect of the parasite's ovipositor is precluded when the entire larval host population is ultimately forced into the areal range of the parasite.

In *Ephestia-Idechthis* ecosystems in which each allotment of wheat is 55 mm in depth instead of 14, its entire consumption does not force any of the host population into the areal range of the parasite. In such a system the average monthly parasitization is about 65%.

It is clearly shown in the 3-year life of the *Ephestia-Idechthis* ecosystem that predation can modify the host-parasite interaction so that host survival increases. Host-egg feeding by the mite and the parasitization of the host larvae by *Idechthis* form a type of interspecific

competition which results in greater host survival than with the parasite alone.

Such a situation may rarely occur under natural conditions. Smith (1929) has pointed out that several natural enemies may have a superior "balancing" effect over a single one since adverse environmental factors are not likely to affect all the natural enemies in the same degree either in time or in space.


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## STOMACH CONTENTS OF A KIT FOX

An adult female kit fox (*Vulpes macrotis neomexicana*) was found dead about 5:00 P.M., December 21, 1958, along US Highway 70, 25 miles west of Las Cruces, Dona Ana County, New Mexico. The specimen was in good condition; the skull was slightly crushed in the parietal and occipital regions. The animal had apparently been killed by a car in the early morning of the same day. This specimen was of average size (710-285-124-82) and given catalog number 2 in the collection of the Stovall Museum, University of Oklahoma.

The stomach of this fox was examined, and it contained 2 small horned toads, *Phyronosoma* sp 45 mm long; 3 *Peromyscus maniculatus;* 18 *Perognathus flavus* in a good state of preservation, and a small immature mouse (head and body 20 mm) which could not be identified. There was enough hair and partially digested remains in the pyloric region of the stomach to suggest 2 or 3 more mammals. The fox must have been killed immediately after feeding. The prey were swallowed whole; the only indication that they had been bitten was the presence of one or two broken areas on the tail and the slightly crushed condition of some of the skulls. No blood or breaks in the flesh were evident.

Two *Perognathus* and one *Peromyscus* were placed in 10% formaldehyde in order that identification could be made in the laboratory. It was later noticed that the pouches of the two preserved pocket mice were full of small seeds. The stomach contents of the mice could only be identified as fragments of masticated seeds. The contents of the cheek pouches were identified as: 141 Needle Gramma seeds (*Bouteloua aristoides*), 21 Russian Thistle seeds (*Salsola kali* var. *tenuifolia*), and 21 "football-shaped" seeds which were probably a Drop-seed (*Sporobolus* sp.). Not only did the cheek pouches contain seeds, but also small pieces of rounded feldspar and quartz which were the same size and shape as the seeds of *Sporobolus*.

Bailey (1931:298) noted that the range of the kit fox is closely correlated with the range of *Dipodomys spectabilis*, and it was thought to comprise a large share of the fox's diet. Although the characteristic mounds of earth suggesting *D. spectabilis* were present, I was unable to collect any specimens from the mounds. However, *D. merriami* and *Perognathus flavus* were obtained (Dec. 22, 1958) from this area, but no remains of *Dipodomys* could be identified in the stomach of this fox.

The food habits of the kit fox are little known, and the remains of large prey found about the dens may be deceiving since the kit foxes apparently swallow much of their food whole. This observation illustrated rather dramatically a food chain in which the herbivorous pocket mice possessed in their cheek pouches the common available seeds of the area, and also, the presence of many of these mammals which obviously had been eaten by the fox within a relatively short period of time.

The author is grateful to Dr. George J. Goodman of the Department of Plant Sciences for the identification of the seeds.


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## MOVEMENTS AND HOME RANGE OF THE GRAY SQUIRREL *SCIURUS CAROLINENSIS*, IN TWO MARYLAND WOODLOTS[1]

Every animal in a given type habitat has a minimal space requirement which must supply its food, shelter and other necessities. The suitability of the habitat, therefore, may determine the extent of the required space and how much the animals must move about in search of the requirements. The purpose of this study was to learn the extent of movements of individual squirrels. Did squirrels forage widely through the forest or did they confine their activities to a small circumscribed area?

[1] A contribution from the Laboratory of Animal Behavior, School of Hygiene and Public Health, The Johns Hopkins University. A portion of Pittman-Robertson Wildlife Research Project W-32-R, Maryland Game and Inland Fish Commission. Contribution No. 128, Md. Dept. Research and Education.

This study was conducted over a period of 3 years, 1952 to 1955, in two 10-acre woodlots belonging to a hospital north of Baltimore. These woodlots were mature stands of large trees of oak, hickory, beech and yellow poplar, some of which were up to 4 feet in diameter. Each woodlot was relatively isolated from other woodlots, greatly restricting movements of squirrels to and from other forest land.

## Methods

A grid was laid out in each woodlot with large white stakes at 100 foot intersections and mimeographed maps were prepared showing the grid and prominent landmarks in each woodlot. These were used to locate captures and observations of squirrels.

Squirrels were captured in 20 to 30 box traps placed at likely spots throughout each woodlot. The trapping periods usually lasted about a month and during this time the traps were frequently moved about within the woods. Every squirrel that was captured was marked with a fur dye (Nyanzol A). In addition the hairs on the distal portion of the tails on males and the hairs on the proximal portion of the tails of females were trimmed with scissors. By using a combination of marking patterns for individuals (Figure 1), it was possible to recognize with binoculars most of the marked individuals seen in the woods. Whenever a squirrel was seen or captured the exact location was denoted on a map.

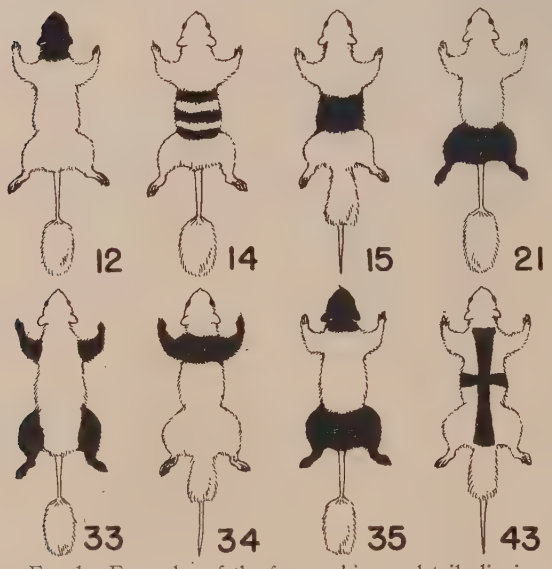


Fig. 1. Examples of the fur marking and tail clipping patterns used to mark squirrels for identification of individuals in the field.

## Results

Repeated captures and observations of individual squirrels gave data on the movements of the animals. Plotting the captures and sight records of individuals on separate maps produced an outline of the animal's home range when the outermost points were connected (Figure 2). The greater the number of recaptures, the nearer this outline approaches the animal's home range. However, trapping can not give more than a crude idea of an animal's home range, because the relatively few times that an animal can be caught is an extremely small representation of the total time the animal spends in the area.

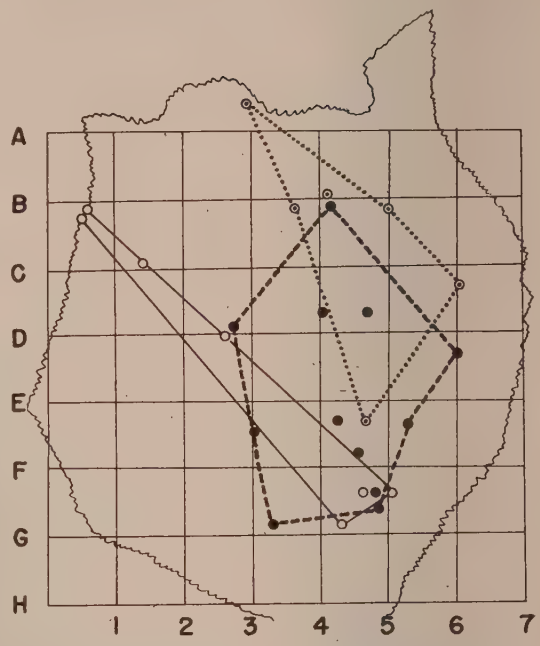


Fig. 2. Map of the north woods showing the 100 foot interval grid and the home range of three squirrels.
⊙ recaptures (and observations) of squirrel #74 (1.15 acres)
● repcaptures (and observations) of squirrel #45 (0.68 acres)
○ recaptures (and observations) of squirrel #64 (2.10 acres)

Fifty-six squirrels with 5 or more recaptures (Table I) had an average home range of 1.4 acres. The average home range (of animals with 5 or more records) for 20 adult males was 1.9 acres, for 18 adult females 1.2 acres, and for 18 immatures 0.9 acres. At first glance, one might conclude that an age and sex difference exists. However, males were captured more often than were females and, since the size of home range generally increases with the number of records, the larger estimated range of males may perhaps be attributed to the greater number of recaptures rather than to actual difference in size of the home range. An analysis of covariance with the number of recaptures as covariant (Table II) showed no significant difference between the size of the home range of adult males, adult females, and immatures.

Because the apparent size of home range is determined to a great extent by the number of recaptures this method is not an entirely satisfactory measure of an animal's range of movements. It is necessary to have at least 3 different points at which an animal was captured or seen in order to get a measurement of area. Five was arbitrarily selected as the minimal number of points used to determine home range. This is not meant to imply that for squirrels with more than 5 records the size of home range was not partially dependent upon the number or recaptures. Only 57 out of a total of 177 squirrels were recaptured or seen more than 5 times so many data are lost when animals with less than 5 recaptures are discarded.

A method which does not discard as many data is to measure the distance between one capture (or observa-

TABLE I. Size in acres of home ranges of 56 squirrels and the number of points on the map used to compute this range.

| Adult Males | | Adult Females | | Immatures | |
|---|---|---|---|---|---|
| Number of Points | Range in Acres | Number of Points | Range in Acres | Number of Points | Range in Acres |
| 5 | 0.2 | 5 | 0.2 | 5 | 0.2 |
| 10 | 0.4 | 6 | 0.2 | 7 | 0.2 |
| 8 | 0.7 | 5 | 0.5 | 7 | 0.3 |
| 5 | 0.7 | 7 | 0.5 | 5 | 0.3 |
| 11 | 0.8 | 8 | 0.6 | 8 | 0.4 |
| 6 | 0.9 | 6 | 0.6 | 7 | 0.4 |
| 5 | 1.1 | 9 | 0.9 | 6 | 0.4 |
| 7 | 1.1 | 8 | 1.0 | 10 | 0.4 |
| 12 | 1.5 | 14 | 1.0 | 8 | 0.5 |
| 18 | 1.5 | 5 | 1.0 | 5 | 0.7 |
| 25 | 1.9 | 9 | 1.2 | 7 | 0.8 |
| 11 | 2.2 | 14 | 1.2 | 5 | 0.8 |
| 9 | 2.4 | 11 | 1.6 | 10 | 1.2 |
| 18 | 2.5 | 7 | 2.0 | 5 | 1.7 |
| 17 | 2.5 | 19 | 2.0 | 12 | 1.7 |
| 16 | 2.5 | 13 | 2.1 | 10 | 1.8 |
| 9 | 2.7 | 13 | 2.1 | 13 | 2.2 |
| 16 | 2.8 | 12 | 2.6 | 13 | 2.9 |
| 5 | 2.8 | | | | |
| 11 | 7.2 | | | | |
| Means | | | | | |
| 11.2 | 1.9 | 9.5 | 1.2 | 7.9 | 0.9 |

TABLE II. Analysis of covariance on the size of home range of adult males, of adult females and of immatures of both sexes with number of recaptures as covariant.

| | | | | | Residual | | | |
|---|---|---|---|---|---|---|---|---|
| Variation due to: | $SS_x$ | $SP_{xy}$ | $SS_y$ | d.f. | SS | d.f. | M.S. | F |
| Classifications | 93.497 | 28.478 | 9.299 | 2 | 4.091 | 2 | 2.046 | 1.99 |
| Squirrels | 990.348 | 102.175 | 64.911 | 54 | 54.370 | 53 | 1.026 | |
| Classifications—squirrels | 1,083.395 | 130.653 | 74.210 | 56 | 58.461 | 55 | | |

$F_{.95}(2, 40) = 3.23$

tion) and the next, because all the data can be used for animals that have been seen or captured more than once. This figure is an index to the extent of movements of animals and has the advantage of not being dependent upon the number of records on that animal. Although these 2 figures (home range and distance between recaptures) are not comparable, one being a linear measurement and the other an areal measurement, they do supplement each other. The distance between recaptures does not give usuable data on a particular individual but is an average index for all the animals at that particular location and time. Movement within the home range cannot be distinguished from dispersal movements and, since animals do not travel in straight lines, it does not estimate actual movements. Both methods are subject to the effects of the spacing of traps, the probability that some animals wander outside of the trapping area, and the possibility of an animal becoming addicted to a particular trap.

The distances between one observation and the next on the maps of the individual squirrels were recorded resulting in a total of 561 measurements. Because these measurements included both sight records and captures in traps there were 3 possible arrangements of the data, (1) the distance between two captures, (2) the distance between a capture and sight record, and (3) the distance between 2 sight records (Table III). The average distance between two captures was 187 feet, between a capture and sight record was 207 feet, and between 2 sight records was 132 feet. An analysis of variance (Table IV) on the 3 groups showed a significant difference among these. Such a difference is expected among the groups because:

TABLE III. Numbers of squirrels captured at various distances as measured from one record to the next.*

| Distance in feet | Number between 2 captures | Number between a capture and sight record | Number between 2 sight records |
|---|---|---|---|
| 0- 5 | 34 | 4 | 8 |
| 6- 45 | 16 | 10 | 6 |
| 46- 95 | 47 | 18 | 11 |
| 96-145 | 69 | 28 | 8 |
| 146-195 | 54 | 26 | 8 |
| 196-245 | 47 | 20 | 7 |
| 246-295 | 25 | 12 | 3 |
| 296-345 | 20 | 11 | 1 |
| 346-395 | 13 | 5 | 1 |
| 396-445 | 8 | 4 | 0 |
| 446-495 | 2 | 5 | 1 |
| 496-545 | 5 | 4 | 0 |
| 546-595 | 0 | 0 | 0 |
| 596-645 | 3 | 0 | 0 |
| 646-695 | 5 | 1 | 1 |
| 696-745 | 2 | 1 | 0 |
| 746-795 | 3 | 3 | 0 |
| 786-845 | 0 | 0 | 0 |
| 846-895 | 1 | 0 | 0 |
| Total.... | 354 | 152 | 55 |

* Records of squirrels seen or caught were marked on individual map records. These dots were numbered consecutively from one (the first capture) to as high as 25. The distance from one dot to the next was measured on the map and converted to feet and arranged in the above table.

TABLE IV. Analysis of variance on movement data collected by three different methods.

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | F |
|---|---|---|---|---|
| Between methods | 2 | 229,263.89 | 114,631.95 | 4.340 |
| Between squirrels | 178 | 4,700,579.34 | 26,407.75 | 1.192 |
| Within squirrels | 382 | 8,457,366.37 | 22,139.70 | |
| Total | 562 | 13,387,209.60 | 23,820.66 | |

$F_{.95}(2, 120) = 3.07$

$F_{.95}(120, 120) = 1.35$

1. Squirrels became habitual visitors of certain traps
2. A squirrel seen on one occasion was likely to be seen in the same spot on later dates because it may have been more conspicuous in that spot and because the observer tends to look for animals in spots where they have been seen before
3. A squirrel's range is 3 dimensional and the range in trees (most sight records were from trees) may have been different from that on the ground (trap records).

It is evident that, if a squirrel were captured a large proportion of the time in one trap, or seen in the same

TABLE V. Distances between recaptures of squirrels arranged according to sex, age and season.

| | IMMATURES OF BOTH SEXES | | | | ADULT FEMALES | | | | ADULT MALES | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Distance in feet | Spring | Summer | Fall | Winter | Spring | Summer | Fall | Winter | Spring | Summer | Fall | Winter |
| 0-5 | 1 | 3 | 1 | 0 | 5 | 1 | 0 | 3 | 2 | 3 | 1 | 2 |
| 6-45 | 0 | 1 | 2 | 1 | 3 | 1 | 1 | 0 | 2 | 1 | 0 | 0 |
| 46-95 | 3 | 4 | 8 | 3 | 2 | 1 | 0 | 4 | 5 | 4 | 5 | 3 |
| 96-145 | 6 | 4 | 5 | 4 | 4 | 7 | 0 | 3 | 6 | 6 | 2 | 4 |
| 146-195 | 6 | 2 | 6 | 5 | 4 | 5 | 0 | 2 | 4 | 6 | 1 | 1 |
| 196-245 | 7 | 1 | 1 | 5 | 3 | 4 | 0 | 2 | 5 | 5 | 1 | 3 |
| 246-295 | 2 | 1 | 1 | 0 | 0 | 3 | 1 | 3 | 6 | 1 | 0 | 1 |
| 296-345 | 1 | 0 | 1 | 2 | 2 | 4 | 0 | 2 | 2 | 2 | 0 | 0 |
| 346-395 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 3 | 2 | 1 | 0 |
| 396-445 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 4 | 0 | 0 | 0 |
| 446-495 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 496-545 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 |
| 546-595 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 596-645 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| 646-695 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| 696-745 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| 746-795 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| 796-845 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 846-895 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Totals | 27 | 16 | 25 | 22 | 25 | 31 | 4 | 20 | 40 | 36 | 11 | 16 |
| Av. distance | 176.7 | 103.1 | 126.4 | 183.2 | 138.2 | 262.9 | 250.0 | 163.0 | 213.0 | 241.9 | 124.5 | 196.9 |

spot on several occasions, the average distance between records would be lowered. On the other hand the location at which a squirrel was captured in a trap would have much less influence on where the observer might see the animal on a subsequent day. Similarly, the spot where a squirrel was seen would also have little effect on which trap would capture the animal. Naturally animals would be seen or trapped only within their range of movements and an animal more active in a portion of its range would be more likely to be seen or captured in this area. Nevertheless, the average distance between a sight record and a trap record is subject to less bias.

It was also suspected that a seasonal difference might exist with respect to the extent of movements (Table V). An analysis of variance was performed using trap records (Table VI). Only trap records were used because of the difference shown to exist between data collected by different methods. Also, the amount of data collected by the other methods was inadequate. The tests were run separately on adult males, adult females and immatures and a significant difference was found between seasonal movements for adult females and for immatures but not for adult males. This test indicated that adult females moved the greatest distance in the summer and the shortest distances during spring. It is possible that in the spring, when they have young, nursing females tend to remain near their nests. In the summer, when the young are no longer dependent on their mothers, the females are free to move about to a greater extent. Females may also move about more during the summer estrous period. The difference existing among the seasons for immature squirrels may be due to the maturation of the animals with consequent longer movements as they become older. Such an age effect existed would influence these data because most of the young squirrels were captured during the fall of 1954 and followed, as they matured, through the following winter and spring. The available food supply could have an effect on movements because, for example, if there is an abundant acorn crop the squirrels would not have to forage as far as when there are few acorns.

It is of interest to note that, during the course of this study in which 177 squirrels were marked, there was no evidence that any of the native squirrels ever wandered across the 1/3-mile distance between the 2 woodlots.

## DISCUSSION

Robinson and Cowan (1954), from a study of the gray squirrel on Vancouver Island, British Columbia found that male squirrels moved over an area of at least 50 to 55 acres and that females moved over an area of 5 to 15 acres. The authors give no indication of how the data that are the basis for these conclusions were collected. However, even if their methods were very different from those used in this study, it is improbable that such a difference could be due to the manner of data collection. The habitat of the Vancouver animals was quite different from the Baltimore area both in vegetation and the amount of actual habitat available. The density of Vancouver Island Squirrels was about 45 squirrels on 50 acres compared with 50 to 60 squirrels on 10 acres in Baltimore. Perhaps the difference can be explained by these differences in habitat and population densities.

In the forests where this study was conducted, squirrels were found to occupy relatively small overlapping home ranges ranging from 0.2 acres to 7.2 acres. Studies of movements of other mammals and birds have shown that the individual animal usually occupies a definite area for its entire adult life. There is a good reason for spending a lifetime in one place. The individual becomes well acquainted with the locality and learns where and how to run to escape danger, where food can be found, and how to get from one place to another within the range. An indication that squirrels become acquainted with their home area is shown by the existence of rigid travel lanes through the tree tops. The same individuals, on a number of occasions, used what appeared to be identical routes through the trees. These routes were often exceedingly indirect and although the route was inefficient, by human standards, such behavior does indicate familarity with the area.

TABLE VI. Analysis of variance of seasonal movements of squirrels based on the distances between recaptures.

IMMATURES

| Source of Variation | Degrees of Freedom | Sum of Squares | Mean Square | F |
|---|---|---|---|---|
| Between seasons | 3 | 92,368.54 | 30,780.51 | 2.92 |
| Between animals | 43 | 452,630.35 | 10,526.29 | 1.56 |
| Within animals | 43 | 289,766.67 | 6,738.76 | |
| Total | 89 | 834,765.56 | | |

$F_{.95}(40, 40) = 1.69$

$F_{.95}(3, 40) = 2.84$

ADULT MALES

| | | | | |
|---|---|---|---|---|
| Between seasons | 3 | 120,039.83 | 40,013.28 | 1.13 |
| Between animals | 37 | 1,306,191.02 | 35,302.46 | 1.29 |
| Within animals | 62 | 1,700,629.35 | 27,429.50 | |
| Total | 102 | 3,126,860.20 | | |

$F_{.95}(3, 40) = 2.84$

$F_{.95}(40, 60) = 1.59$

ADULT FEMALES

| | | | | |
|---|---|---|---|---|
| Between seasons | 3 | 255,294.48 | 85,098.16 | 3.65 |
| Between animals | 34 | 792,680.49 | 23,314.13 | 0.89 |
| Within animals | 42 | 1,094,922.22 | 26,069.58 | |
| Total | 79 | 2,142,897.19 | | |

$F_{.95}(30, 40) = 1.74$

$F_{.95}(3, 30) = 2.92$

An animal that is outside of its area of familiarity does not know where to run when danger threatens. This uncertainty is strikingly shown by the way animals behave when released in a strange environment. Alien squirrels trapped in the city of Baltimore did not know where to run when released in these woodlots whereas the resident squirrels when released disappeared in short order (Flyger 1955). This same behavior of animals released in a strange environment has been observed in other species. D. E. Davis (verbal communication) has described such behavior in Norway rats and I have witnessed cottontail rabbits running about in a bewildered manner for long distances when released in a strange place.

Wildlife workers frequently speak of squirrels exhibiting a fall reshuffle of home ranges and of moving long distances. Undoubtedly, squirrels do wander long distances, and at times shift their home ranges, but this is probably true to a small degree rather than being the rule. Considering the fact that many mammals occupy rigid home ranges, it seems improbable that squirrels would differ and wander great distances or change their home ranges every fall. It might happen that, on occasion, a squirrel becomes lost when straying outside of its area of familiarity, and if there is no sense of orientation it might wander aimlessly, reaching home only by chance.

There exist many references in the literature to extensive mass movements of gray squirrels. The mass movements for which gray squirrels are famous have never, to my knowledge, been critically studied by a biologist, nor do the results of this research shed any light on this phenomenon. Until a squirrel emigration is actually studied by a biologist this aspect of squirrel behavior will remain a mystery.

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## AN ESTIMATE OF THE INTRINSIC RATE OF NATURAL INCREASE IN THE PLANARIAN, *DUGESIA TIGRINA*

The utility of the intrinsic rate of natural increase[1] as a parameter combining the reproductive rate, mortality, and stable age distribution of a species in a particular environment is well established. It has been used as a measure of population growth (Lotka 1943) and as a quantitative expression of the relative favorability of experimental conditions in studies on population dynamics and limiting factors (Birch 1948, Leslie and Park 1949). Most recently, it has been suggested that the intrinsic rate of natural increase under optimal conditions reflects the adversity of the environment or niche in different species (Evans and Smith 1952). The subject has been reviewed by Smith (1954) and Cole (1954), and further theoretical conclusions were drawn by them.

The complete life table and intrinsic rate of natural increase are now known for various species of bacteria,

[1] The intrinsic rate of natural increase is defined as the rate of increase per individual in a population which has attained a stable age distribution, or as r in the equation for exponential growth:

$$\frac{dN}{dt} = rN,$$

where N = number of individuals and t = time.

protozoa, arthropods, mollusks, and mammals (Deevey 1947, Smith 1954). The following observations on the planarian, *Dugesia tigrina,* were carried out in order to provide comparable population data for an asexual, predacious metazoan.

This investigation was undertaken to fulfill part of the requirements for the Honors Degree in Zoology at the University of Michigan. The author wishes to express his appreciation for the sound guidance and generous facilities extended to him by Dr. F. E. Smith and to Drs. N. G. Hairston, F. A. Pitelka, and L. C. Cole for their helpful suggestions concerning the manuscript.

## Methods

The 2 clones of *D. tigrina* which were studied were started with 2 newly formed fission products (tails) from a laboratory population which had been under casual observation for at least 2 months. None of the individuals of this population has ever been observed to reproduce sexually. These individuals were placed in separate finger bowls filled with conditioned water and containing an abundance of *Daphnia magna* as a food source. The water was maintained at a relatively constant temperature of 23°C throughout the period of the investigation. Daily observations were made, and records kept of any fission or mortality which occurred in the cultures. When tails were found, they were removed to separate finger bowls, where their life histories were followed.

The water and food supply were changed every 3rd day, because it was found that failure to do so resulted in the degeneration and ensuing death of the individual concerned. Fission and death rates obtained from cultures in which the water was changed daily were not significantly different from those observed under the above conditions. That this constitutes an optimum environment for *D. tigrina* cannot be substantiated, but observations in the laboratory and field suggest that they approximate it, at least for this type of food.

## Results

Using the above procedure, the individual life histories of 26 flatworms were followed for periods ranging from 44 to 107 days. From these data it was possible to construct a life table for each individual, and compute its intrinsic rate of natural increase (r). The method of Birch (1948) for approximating this parameter was employed. This procedure involves the use of trial values of r to find that which satisfies the equation: $\Sigma e^{-rx} l_x m_x = 1$ (where $l_x$ equals the probability at "birth" of being alive at age x, and $m_x$ is the mean number of tails produced per day by an individual aged x). Estimates of r were picked such that their summations would bracket unity for any individual. The actual values of r were then obtained by the graphical solution proposed by DeWitt (1954), and these are presented in Table I.

A mean intrinsic rate of 0.072 was obtained when the data were treated on an individual basis, the differences in the intrinsic rates between the two clones not being significant as determined by a non-parametric statistical test (Mann-Whitney U.). This made it possible to treat all the individuals as a single clone and thereby construct a life table for the entire population (summarized in Table II). When the above equation was applied to these data, treated as a single population, an intrinsic rate of 0.072 (the same value as the mean r for individuals) was obtained. Since the tails took longer to reach reproductive age than the heads (Table III), it was not possible to consider *Dugesia* as an example of binary fission or to employ a "generation law" (Thompson 1931, Cole 1954) in calculating r on a population basis.

Table I. The intrinsic rate of natural increase for individuals of *Dugesia tigrina.*

| Clone $A_2$ | | | Clone $B_2$ | | |
|---|---|---|---|---|---|
| Individual | Intrinsic rate (r) | Days under observation | Individual | Intrinsic rate (r) | Days under observation |
| 2.0 | 0.084 | 107 | 2.0 | 0.075 | 107 |
| 2.1 | 0.075 | 95 | 2.1 | 0.073 | 89 |
| 2.2 | 0.080 | 84 | 2.2 | 0.071 | 84 |
| 2.3 | 0.053 | 63† | 2.3 | 0.059 | 80 |
| 2.4 | 0.062 | 79 | 2.4 | 0.071 | 76 |
| 2.5 | 0.077 | 74 | 2.5 | 0.092 | 71 |
| 2.6 | 0.062 | 62† | 2.6 | 0.089 | 67 |
| 2.7 | 0.077 | 68 | 2.7 | 0.059 | 62 |
| 2.8 | 0.084 | 64 | 2.8 | 0.072 | 59 |
| 2.9 | 0.051 | 61 | 2.9 | 0.000 | 51† |
| 2.10 | ..... | 40† | 2.10 | 0.072 | 50 |
| 2.11 | 0.091 | 53 | 2.11 | 0.076 | 47 |
| 2.12 | 0.074 | 46 | 2.12 | 0.056 | 44 |

† Died.

Table II. Averaged age specific survivorship ($l_x$) and reproductive ($m_x$) rates for laboratory clones of *Dugesia tigrina.*

| Age group (in days) | Pivotal age (x) | $l_x$* | $m_x$ | $l_x m_x$ |
|---|---|---|---|---|
| 1-4 | 2 | 1.0000 | 0.0000 | 0.0000 |
| 5-8 | 6 | 1.0000 | 0.0000 | 0.0000 |
| 9-12 | 10 | 1.0000 | 0.0866 | 0.0866 |
| 13-16 | 14 | 1.0000 | 0.1154 | 0.1154 |
| 17-20 | 18 | 1.0000 | 0.1443 | 0.1443 |
| 21-24 | 22 | 1.0000 | 0.1635 | 0.1635 |
| 25-28 | 26 | 1.0000 | 0.1923 | 0.1923 |
| 29-32 | 30 | 1.0000 | 0.1539 | 0.1539 |
| 33-36 | 34 | 1.0000 | 0.1731 | 0.1731 |
| 37-40 | 38 | 0.9808 | 0.2066 | 0.2019 |
| 41-44 | 42 | 0.9608 | 0.1638 | 0.1573 |
| 45-48 | 46 | 0.9570 | 0.1221 | 0.1169 |
| 49-52 | 50 | 0.9194 | 0.1251 | 0.1147 |
| 53-56 | 54 | 0.9274 | 0.1053 | 0.0970 |
| 57-60 | 58 | 1.0000 | 0.1360 | 0.1360 |
| 61-64 | 62 | 0.8865 | 0.0909 | 0.0802 |
| 65-68 | 66 | 0.8513 | 0.1136 | 0.0962 |
| 69-72 | 70 | 0.8744 | 0.0750 | 0.0663 |
| 73-76 | 74 | 0.8945 | 0.1806 | 0.1611 |
| 77-80 | 78 | 0.8695 | 0.1503 | 0.1305 |
| 81-84 | 82 | 1.0000 | 0.0000 | 0.0000 |
| 85-88 | 86 | 1.0000 | 0.1250 | 0.1250 |
| 89-92 | 90 | 1.0000 | 0.1667 | 0.1667 |
| 93-96 | 94 | 1.0000 | 0.1250 | 0.1250 |
| 97-100 | 98 | 1.0000 | 0.0000 | 0.0000 |
| 101-104 | 102 | 1.0000 | 0.1250 | 0.1250 |
| 105-107 | 106 | 1.0000 | 0.2500 | 0.2500 |
| | | | | $\Sigma = 11.7141$ |

* The dip in the $l_x$ values results from the sample being made up of different age classes at any one time. Thus those individuals which died can be considered only to the age they would have been when the experiment was terminated and therefore do not enter into the $l_x$ calculations at the later time intervals.

It should be noted that the survival ($l_x$) of *D. tigrina* remained quite high throughout the course of this investigation; *i.e.,* the data were obtained for only part of the life span of most individuals. Since the equation

TABLE III. Time intervals between successive transverse fissions in a laboratory population of *Dugesia tigrina*.

| Fission | Mean interval in days | Standard deviation | Extremes | Sample size |
|---|---|---|---|---|
| First | 15.1 | 2.95 | 10-20 | 21 |
| Second | 6.3 | 2.15 | 3-11 | 20 |
| Third | 5.2 | 1.96 | 3-11 | 20 |
| Fourth | 5.6 | 2.60 | 3-11 | 17 |
| Fifth | 5.0 | 2.00 | 2-13 | 17 |

used in estimating r calls for a sum of $e^{-rx}l_xm_x$ values over the entire life span of the population, it would appear that the estimates of intrinsic rate are too low. However, at later time intervals (x), the value of $e^{-rx}$ becomes so small that any change in birth ($m_x$) or death ($l_x$) has an insignificant influence on the summation. To determine the magnitude of this error, cumulative sums of $e^{-rx}$ were computed for values of r which bracketed those already found for individuals. By taking the percent age of the sum contributed by successive time intervals, it was possible to observe the time at which 90% of this contribution to $\Sigma e^{-rx}$ had been made. Thus it was found that when r equaled 0.05, observations carried on past the 45th day would result in a maximum increase in r of 10% (Figure 1). Since the mean intrinsic rate is higher than 0.05 and no individual was observed for less than 44 days (the majority being followed for 60 days or longer), it would appear that the incomplete life table does not constitute a significant error in this case.

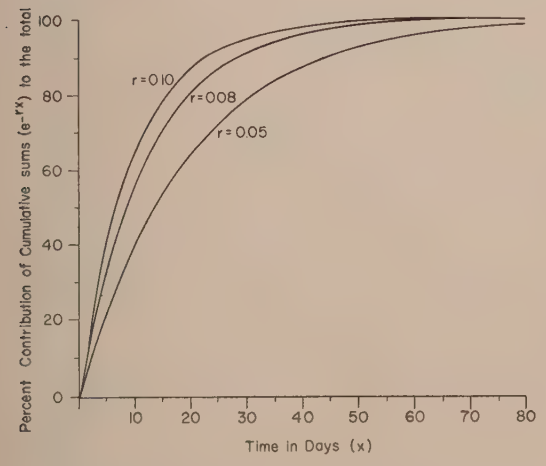


FIG. 1. Contribution made by cumulative sums of $e^{-rx}$ at successive time intervals to the total sum of $e^{-rx}$.

On the other hand, the fact that the data do not cover an entire generation makes it impossible to calculate the net reproductive rate ($R_0$), which has been defined as the ratio of reproductive offspring "born" in two successive generations or as the sum of the $l_xm_x$ column of a completed life table (Birch 1948). When this summation is made using the data in Table II, a value of 11.71 is obtained. While this is not comparable with published net reproductive rates, it does show that on the average, an individual *D. tigrina* will give rise to 11.7 tails during the 107 days after "birth."

## DISCUSSION

That reproductive capacities are subject to natural selection has become generally accepted since Darwin's time. Cole (1954) has reviewed this subject and some of its implications in the light of recent theories in population dynamics.

Since most species maintain relatively stable population sizes through time, it follows that a species would evolve an intrinsic rate equal to zero under the stresses of its natural environment and that every adult would be replaced by about one individual in the next generation; *i.e.*, $R_0 = 1$. Thus, Evans and Smith (1952) were able to conclude that the distance the maximal r deviates from zero reflects "the degree to which the natural environment departs from conditions conducive to greatest growth" and the magnitude of $R_0$ under optimal conditions "indicates the rigorousness of the natural environment in terms of individual replacement." As shown above, it is possible for a life table to progress to a point at which individuals become "immortal" in terms of their contribution to population growth. While it is impossible to measure $R_0$ at this point, r is approaching a constant and is thus the only population parameter available for comparative purposes.

To claim that the value of r obtained for *Dugesia tigrina* under the described conditions is maximal would entail taking observations at all the various combinations and intensities of the variables that influence planarian populations. Pilot experiments at different temperatures and light intensities and the elimination of intraspecific competition by isolating the individuals suggest, however, that the r values obtained at least closely approach a maximum for this food source. This makes possible a rough comparison of the intrinsic rate for *D. tigrina* with those suggested by Evans and Smith (1952) as also approaching the maximum (Table IV). In comparison, *D. tigrina* has an intrinsic rate which is not excessively high for an animal of its size and phylogenetic position. Thus it would appear that it lives in an environment which is moderately safe in terms of population growth.

TABLE IV. Comparison of the intrinsic rate of natural increase and net reproductive rate for various animal species.

| Species | Intrinsic rate (r/day) | Net reproductive rate (Ro) | Source of data |
|---|---|---|---|
| Microtus agrestis | 0.0125 | 5.904 | Leslie and Ranson 1940 |
| Rattus norvegicus | 0.0147 | 25.66 | Leslie 1945 |
| Physa gyrina | 0.0457 | 418.0 | DeWitt 1954 |
| Dugesia tigrina | 0.072 | ..... | Root 1960 |
| Tribolium castaneum | 0.101 | 275.0 | Leslie and Park 1940 |
| Calandra oryzae | 0.109 | 113.56 | Birch 1948 |
| Pediculus humanus | 0.111 | 30.93 | Evans and Smith 1952 |

This conclusion is substantiated by Hyman's report (1951, p. 194) that planarians have few predators because of their distasteful surface secretions. Casual observations of laboratory populations maintained at low food levels suggest that cannibalism exerts a major population control only at higher densities.

Reproductive potential is determined by natural selection acting on life history features such as length of the pre-reproductive period, physiological longevity, and litter size. The interrelations between these variables have been discussed in detail by Birch (1948) and Cole (1954). There are limitations, however, of the degree to which life events can be modified to increase the intrinsic rate. For instance, it was observed under laboratory

conditions that an individual which shortened its pre-reproductive period by undergoing fission before the 10th day gave rise to fragments that were too small to feed on *Daphnia magna* and therefore starved. In contrast, the apparent advantage of increasing "litter size" by shifting to sexual reproduction would be partially offset by an accompanying increase in the length of the pre-reproductive period. Thus, while transverse fission can increase r by shortening the pre-reproductive period, it must continue for a long time in order to contribute substantially to the $R_0$. This is demonstrated by the *D. tigrina* life table in which reproduction continues to add to the $R_0$ after its contribution to r is no longer important.

SUMMARY

A life table and the intrinsic rate of natural increase for laboratory populations of *Dugesia tigrina* feeding on *Daphnia magna* are calculated. The influence on the size of intrinsic rate and other population parameters of reproduction at later time intervals in the life history are evaluated. Important aspects of the life history are discussed as they relate to the reproductive capacity of this species.

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## A NOTE ON POPULATION PARAMETERS IN CASES OF COMPLEX REPRODUCTION

INTRODUCTION

In recent years ecologists have been devoting considerable attention to the ways in which the life history features characterizing particular species or local populations affect the potentialities for population growth and the characteristics of the future population (*e.g.* Birch 1948, Andrewartha and Birch 1954, Cole 1954, Smith 1954). It is important to make such determinations not only for the prevailing schedules of reproduction and mortality observed under specific conditions but also for the ideal schedules theoretically available to a given species under optimum conditions. With these ideal conditions the population would grow at the maximum possible exponential rate and I have proposed elsewhere (Cole 1957) that we employ this maximum value of the intrinsic rate of natural increase as a measure of Chapman's "biotic potential." This is a species characteristic important for success in survival and dispersal and, therefore, potentially subject to natural selection.

A convenient way of computing the value of the intrinsic rate of increase ("r"), which is basic to all of the other population parameters, is to write a "generation law" after the manner of Thompson (1931). From this one can compute the exact size and composition of the population at any time in the future when the initial population is given and the life history pattern remains unchanging. By letting the generation law define a difference equation (Cole 1954) a very easy method becomes available for computing the value of r which, of course, is independent of the size and composition of the initial population.

The simplest possible cases of population growth occur in those semelparous organisms where reproduction is by fission of a parental individual into 2 or more, say "n," daughter individuals. Here, the pattern of potential growth is obvious and the intrinsic rate of increase per generation interval is simply the natural logarithm of n. Hence, for such cases, one would not normally bother to write a generation law.

However, if one were to write a generation law for an organism such as *Amoeba*, it is evident that there would be 2 alternative ways of expressing the life history. On the one hand we might consider that the life of an individual *Amoeba* terminates upon fission at some age a, at which time 2 daughters are produced. The generation law would then become: $G = 2T^a$. Alternatively, one could follow the traditional approach dating back to Weismann (1891) and regard each *Amoeba* as an immortal organism producing one daughter at the end of each time interval of length a. The generation law then would be written as: $G = T^a + T^{2a} + T^{3a} + \ldots$. The 2 approaches must necessarily lead to the same result when used for computing future population size and the value of r.

My reason for considering such elementary matters is that the preceding paper (Root 1960) discusses the intrinsic rate of increase in a species where each repro-

ductive event produces 2 types of individuals which develop at different rates. In this case the 2 ways of looking at the life history are still available to us. It is probably most conventional to regard a flatworm reproducing asexually as an immortal organism but there is also merit in the alternative viewpoint. Fission has a rejuvenating influence on the animal so that the 2 products of division in Planarians or Amoebas are each physiologically younger than the "parent" (Child 1915). For the student of populations it is definitely advantageous to work with finite values for such parameters as the mean length of life and the mean length of a generation.

In Root's experiments with *Dugesia* a tail resulting from division required at least 10 days from "birth" before it would again divide into a head and tail and, for 21 individuals, the average length of this interval was about 15 days. On the other hand, a head could divide into a head and tail in as little as 3 days and, on the average, required about 6 days to reach reproductive maturity.

It is certain that comparable situations will be found to occur in many other species, particularly when asexual reproduction is involved. For example, Mr. Alan Stiven, working with *Pelmatohydra oligactis* in this laboratory, finds that under certain culture conditions (constant light, temperature of 21°C, maximal feeding at 24-hour intervals) a mature Hydra can produce a new bud each day indefinitely but that a new Hydra arising as a bud requires 6 days to reach reproductive maturity. In various algae and flagellates also, the 2 products of binary fission differ morphologically, as when one daughter cell receives a flagellum and the other does not or where, as in many diatoms, the daughter cells differ in size. I have been unable to find data on whether or not these morphological differences are associated with differences in rate of maturation but it is certainly possible that they are. It is even conceivable that reproduction in some cases may lead to the production of varying numbers of several types of offspring differing in maturation rates and it seems desirable to have methods for computing the population parameters in such cases of complex reproduction. It turns out that such cases can be handled quite easily.

## The Case of the Immortal Worm

Let us assume that a *Dugesia* head can bud off a new tail when it has reached some age a but that a tail cannot reproduce until it reaches some greater age b. Now, if we start with a "newborn" head and regard it as immortal, it produces tails on days a, 2a, 3a, . . ., indefinitely. The tail born on day a, in turn, becomes a parent on day a + b which is equivalent to becoming a "newborn" head on day b, or when its parent is b days old. Since reproduction is repeated every a days, we get the generation law: $G = T^b + T^{b+a} + T^{b+2a} + \ldots$ . If we let $P_t$ represent population size on any day t, population size will obey the recurrence formula: $P_t = P_{t-b} + P_{t-b-a} + P_{t-b-2a} + \ldots$ . Treating this recurrence relationship as a difference equation, as described by Cole (1954), the intrinsic rate of increase for this reproductive pattern is the single positive value of r satisfying the equation: $e^{rt} - [e^{r(t-b)} + e^{r(t-b-a)} + e^{r(t-b-2a)} + \ldots] = 0$. Since $e^{-ra} < 1$, the infinite sum of the expression in brackets is:

$$\frac{e^{r(t-b)}}{1 - e^{-ra}}$$

and the equation reduces to:

$$e^{-ra} + e^{-rb} = 1 \quad (1).$$

This equation can easily be solved for r by successive approximation employing a table of the exponential function.

To find the maximum possible value of r for *Dugesia* under the conditions of Root's observations we take his minimum values a = 3 and b = 10. This gives: $e^{-3r} + e^{-10r} = 1$, from which r = .120, which is well above the value r = .072 estimated by Root from actual laboratory populations. The difference results from the fact that only a few individuals matured at the maximum possible rate and that there was even some mortality.

If we take the average values observed by Root, a = 6 and b = 15, we obtain r = .071 which is nearly identical with his value. This close correspondence, however, is partially accidental. In the actual population, the occurrence of some mortality will tend to reduce the observed value of r but there is another influence that works in the opposite direction; the individuals that mature before average reproductive age will make disproportionately large contributions to the value of r (cf. Cole 1954). In this particular case these 2 opposing influences approximately cancelled each other.

When we consider important population parameters other than the intrinsic rate of increase, this model in which the life span is regarded as infinite is less satisfactory. How are we to compare this species with others in terms of the mean length of life, life expectancy, net reproductive rate, age structure of the stable population, or mean length of a generation? Arbitrary definitions could be made and Root, in fact, computes one kind of value for $R_o$, the net reproductive rate. However, these parameters become much more intelligible and realistic if we use a modified form of the fission model in which the life of each individual is regarded as terminating at the time of division.

## The Case of the Mortal Worm

In developing this model it turns out to be convenient to include greater generality than is needed for considering population growth in *Dugesia*. We shall consider the case where several types of offspring rather than just 2 are produced at each reproductive event and where the various types are not necessarily produced in equal numbers. This latter generalization could be applied to cases of binary fission in forms like *Dugesia* if the probability of survival to reproductive age should differ for "heads" and "tails."

We assume that at each reproductive event the parental individual is replaced by $n_A$, individuals of type A, $n_B$ individuals of type B, $n_C$ individuals of type C, and so on for as many types of offspring with different rates of maturation as are encountered. It will often be convenient to designate the type of individual that matures most rapidly as A. Thus, in *Dugesia,* heads would be the type A offspring and tails would be type B.

It is possible to write a generation law of sorts for this case but the result ($G = n_A T^a + n_B T^b + n_C T^c + \ldots$) lacks some of the simple properties that make generation laws useful (Thompson 1931). In particular, the generating functions for future population (Cole 1954) give results that differ with the initial composition of the population. For the purpose of determining the population parameters it is sufficient to note (as can be verified by direct computation) that population size obeys the recurrence relation:

$$P_t = n_A P_{t-a} + n_B P_{t-b} + n_C P_{t-c} + \ldots . \quad (2)$$

Writing this as a difference equation for r we obtain:

$$e^{rt} = n_A e^{r(t-a)} + n_B e^{r(t-b)} + n_C e^{r(t-c)} + \ldots ,$$

and, multiplying by $e^{-rt}$, we obtain:

$$1 = n_A e^{-ra} + n_B e^{-rb} + n_C e^{-rc} + \ldots \quad (3).$$

Thus, equation (1) above is seen to be merely the special case of equation (3) in which only 2 types of offspring are produced and $n_A = n_B = 1$.

The advantage of this approach lies in the fact that each type of individual has a definite life span so that various population parameters in addition to r can be determined.

The offspring produced at any reproductive event number $n_A + n_B + n_C + \ldots$ and they survive for a total of $an_A + bn_B + cn_C + \ldots$ time intervals. Thus the mean length of life, or expectation of life at birth, is:

$$\overset{o}{e}_o = \frac{an_A + bn_B + cn_C + \ldots}{n_A + n_B + n_C + \ldots} \quad (4).$$

For *Dugesia* this is simply the mean of a and b, 6½ days as a minimum in Root's series and 10½ days on the average.

### Structure of the Stable Population

It is easy to see that the recurrence relation of formula (2), which applies to the total population, applies also to any age or type class within the population. It follows that the growing population must acquire a stable structure such that the proportion of, say, all type A individuals, or all type A individuals of a single age class, in the population does not change with time. It also follows that the proportion ($c_x$) of any population type falling in the age class between ages x and $x + 1$ is given by:

$$c_x = c_o e^{-rx} \quad (5).$$

In formula (5), $c_o$ represents the birth rate per head per unit time and we next consider how to determine its value.

Let us consider a stable population in which the zero age class consists of $A_o$ "newborn" individuals of type A, $B_o$ newborn individuals of type B, $C_o$ of type C, and so on. By virtue of the exponential growth in a stable population, the total number of type A individuals in the population is:

$$A_o \left[ 1 + e^{-r} + e^{-2r} + \ldots e^{-r(a-1)} \right] = A_o \left[ \frac{1 - e^{-ra}}{1 - e^{-r}} \right]$$

Similarly, the total number of type B individuals is $B_o \left[ \frac{1 - e^{-rb}}{1 - e^{-r}} \right]$ and the same form of expression applies to any additional types. Adding all of these expressions together will give us the total population size, and we know the number of newborn individuals which is, $A_o + B_o + C_o + \ldots$.

Then, the ratio of newborn to total population (the population birth rate) is:

$$\frac{(A_o + B_o + C_o + \ldots)\ (1 - e^{-r})}{A_o\ (1 - e^{-ra}) + B_o\ (1 - e^{-rb}) + \ldots}$$

Since newborn individuals are always produced together in relative numbers $n_A, n_B, n_C, \ldots$, we may write this as:

$$c_o = \frac{(n_A + n_B + n_C + \ldots)\ (1 - e^{-r})}{n_A\ (1 - e^{-ra}) + n_B\ (1 - e^{-rb}) + \ldots}$$

The denominator of this formula is found from equation (3) above to be simply: $n_A + n_B + n_C + \ldots - 1$, and the formula for the birth rate becomes simply:

$$c_o = \frac{(n_A + n_B + n_C + \ldots)\ (1 - e^{-r})}{n_A + n_B + n_C + \ldots - 1} \quad (6).$$

For *Dugesia*, where $n_A = n_B = 1$, the population birth rate is simply:

$$c_o = 2(1 - e^{-r}).$$

As r increases, the population comes to contain many very young individuals. Root's average values, $a = 6$ and $b = 15$, would lead to a stable population containing 13.89% of individuals (heads and tails) under one day old, while the maximum rates of maturation, $a = 3$ and $b = 10$, would lead to a stable population containing 22.62% of these newborn individuals. This illustrates the all too neglected fact that the study of age distribution in natural populations may yield important information about these populations.

In a population of *Dugesia* it might be difficult to age the individuals and thus work out the age structure of the population. It might, however, be possible to classify all individuals as heads or tails, and the composition of the population with respect to this criterion is also of potential interest.

By the same reasoning that led to equation (6) the birth rate for any type of individual, say type A, is given by:

$$c_o\ (A) = \frac{n_A\ (1 - e^{-r})}{n_A\ (1 - e^{-ra}) + n_B\ (1 - e^{-rb}) + \ldots}$$

which, for *Dugesia*, reduces to:

$$c_o\ (A) = (1 - e^{-r}) = c_o\ (B).$$

Thus the proportional representation in the total population of individuals of one type, say type A, falling in the age range x to $x + 1$ is:

$$c_x = (1 - e^{-r})\ e^{-rx} l_x \quad (7).$$

For type A, $l_x$ is unity when $x < a$ and zero thereafter. For type B, survivorship is unity up to and including age $b - 1$.

For the proportion of type A individuals (heads) in a *Dugesia* population we have:

$$\sum_{x=o}^{a-1} c_x\ (A) = (1 - e^{-ra}) = e^{-rb} \quad (8).$$

Clearly, the proportion of tails must be: $1 - c_x\ (A) = e^{-ra}$.

This shows that, in a form such as *Dugesia* where $n_A = n_B$, the type of offspring that matures more rapidly must always make up less than ½ of the stable population. For $a = 6$ and $b = 15$, heads would make up 34.69% of the stable population, while $a = 3$ and $b = 10$ would yield a stable population with 30.23% heads.

### The Net Reproductive Rate

$R_o$, the net reproductive rate may be defined as the ratio of numbers of female births in 2 successive generations of a population growing exponentially with stable age and sex structure. As is discussed by Root (1960), its value is commonly determined from the formula:

$$R_o = \sum_{o}^{\infty} l_x m_x \quad (9).$$

Another common way of determining $R_o$ is from the formula:

$$R_o = e^{rT} \quad (10),$$

where T is defined as the mean length of a generation, or average interval between birth of parent and birth of offspring in the stable population. It has, however, been pointed out to me by F. E. Smith that the identity of formula (10) is not necessarily precisely correct unless all reproduction occurs at a single uniform parental age.

In the conceptual model where each *Dugesia* is regarded as immortal it is obvious that formula (9) gives rise to an ever increasing sum and that formula (10) cannot be used because there seems to be no logical way of defining the mean length of a generation. Thus, Root was unable to obtain a value of $R_0$ comparable with values published for species characterized by sexual reproduction and mortality.

In the model of the mortal worm, $l_x$ is everywhere unity up until reproduction and $m_x$ has only one non-zero value, $m_x = 2$. Therefore, formula (9) gives us $R_0 = 2$. Applying this value to formula (10) we obtain $T = 9.76$ days when $r = .071$, and $T = 5.78$ days when $r = .120$. These are the generation lengths that would give these intrinsic rates of increase if heads and tails matured at the same age. It is noteworthy that both values are somewhat below the mean lengths of life as computed from formula (4). This is because heads, maturing more rapidly, produce more offspring than do tails.

It is interesting to compare the numbers of offspring born to heads and to tails in a single time interval. Since the number of offspring per birth is a constant, it is sufficient to find the relative proportions of heads aged $a - 1$ and tails aged $b - 1$ in the stable population. From formula (7), the proportion of mature heads in the population is $e^{-ra}(e^r - 1)$ and the proportion of mature tails is $e^{-rb}(e^r - 1)$. Thus the proportion of heads among the mature individuals or, what is the same thing, the proportion of births arising from heads, is precisely $e^{-ra}$. This, as appears from formula (8), is identical with the proportion of tails in the total population. Similarly, in any time interval, the proportion of the total offspring produced by tails is the same as the proportion of heads living in the stable population.

From formula (8) we can also compute the true mean length of a generation. The proportion of heads in the stable population is $e^{-rb}$ and each of these is going to survive until it reproduces at age a. Therefore, the number of time intervals contributed per head to the total life of this population is $ae^{-rb}$. Similarly, each tail will contribute $be^{-ra}$ intervals, and the mean length of a generation will be the sum of these 2. For $a = 3$ and $b = 10$, we find $T = 7.88$ days and, for $a = 6$ and $b = 15$, we find $T = 11.88$ days.

One would be tempted, in analyzing an actual population where the mean generation length and the intrinsic rate of increase are accurately known, to estimate $R_0$ from formula (10). If we substitute the above values in this formula we find $R_0 = 1.56$ for the more rapidly growing population and $R_0 = 2.32$ for the average rates of maturation. Although formula (10) gives a somewhat ambiguous definition of the net reproductive rate, these results do illustrate one of the potentially misleading properties of $R_0$ (cf. Lotka 1945). A change in the schedule of reproduction that increases the potential rate of population growth may actually result in a decreased value of the net reproductive rate.

Acknowledgments

I wish to express gratitude to Richard B. Root for inspiring this study and permitting use of his data, to Alan E. Stiven for permission to quote unpublished preliminary results, and especially to Dr. Frederick E. Smith of the University of Michigan who, in his capacity as editorial referee, has contributed greatly to improvements intervening between first and final drafts of this paper.

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## A NOTE ON STATIONARY NETS[1]

During the preparations for an experiment on the dispersal of marked mosquitoes in 1952 Provost (1960), the late Mrs. Astrid Tetens Nielsen realized that stationary nets would be a valuable tool for selectively catching mosquitoes having a directional flight. The nets constructed with this idea as a basis (Figure 1), consist of a 2x2 meter wide pyramid-shaped entrance from which random flying individuals in most cases will escape, while individuals carried by the wind or with a definite directional flight will be guided to the opening at the tip of the pyramid and into the long sleeve.

The material used for the pyramid was dark blue

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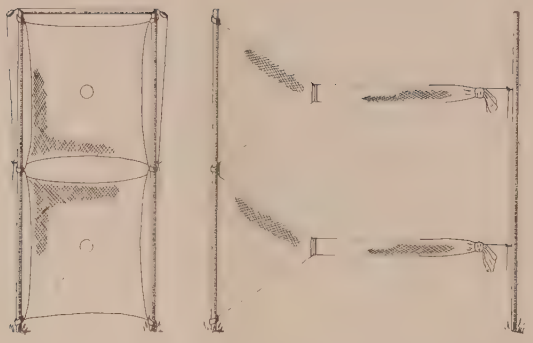

FIG. 1. Sketch of stationary nets used for catching dispersing mosquitoes and migratory butterflies.

nylon netting; the sleeves were of the same material but white.

The tip of the pyramid was fashioned to a circular opening with the material fastened to an embroidery hoop, 18 cm in diameter. The sleeve was cylindrical with a diameter of 18 cm; it was reinforced at the entrance by a similar hoop. To attach the sleeve to the pyramid tip, one of the hoops was slipped into the other. As the hoops were practically of the same size the coupling was able to resist a certain pull but it was found useful to reinforce it by means of a ring of elastic between the two hoops. The other end of the 2½ m long sleeve was closed by a simple knot.

The 4 corners of the entrance to each net were fastened to curtain rings which could move up and down 2 vertical aluminum tubes stuck into the ground and connected at the top. They were secured by guide ropes. Right under the top piece were pulleys by which the nets could be hauled up so that the entrances were kept open. The tail end of the sleeve was kept up in a similar way so that the whole net was kept horizontal. We used to keep the lower edge of the lower net just above ground.

During the dispersal experiment 4 such traps were arranged around the release site. The catches showed that the mosquitoes left with the wind; details will be published elsewhere.

For a few weeks one of the nets was placed on a ridge about 700 meters inland facing east toward the mosquito producing marshes. It was found that the catches in the nets showed changes possibly related to migrations from the marsh.

During the summer of 1957 four nets were placed in a mosquito breeding marsh at the Entomological Research Center. The catches were constantly small, but there was no evidence of migratory flights of mosquitoes during this period.

The sleeves were changed once a day, and it was noticed that during the daytime quite a few *Ascia monuste* were caught in the nets. An outbreak of this migratory butterfly occurred about the first of June in the marshes north of the one with the nets, and a south-going migration was observed during the following days.

June 2, 3, and 4, 98 individuals were caught, 89 of them in the lower north-exposed net. During the 2 first weeks of June, 141 individuals were caught, 86% of them in the same net. In the next 2 weeks only 14 individuals were caught, 12 of which were south-going migrants. Although there still remained a fairly large population around the nets during most of July, only 3 individuals were caught (2 in the north-exposed, lower net). It was observed that resident butterflies frequently entered the funnel but always flew out again without entering the sleeve.

During a recent investigation on the chironomid, *Glyptotendipes paripes*, stationary nets were found to be extremely valuable for the analysis of the flight from the lake to the shore which occurs each evening after sunset. The newly emerged individuals are unable to fly against the wind, and, therefore, are carried by the wind to the shore. The older males, which are able to fly against a fairly strong wind out over the lake to the emergence areas, were, from direct observation, believed to return with the wind. This point was clearly proven by catches in the stationary nets which also provided a clear picture of the sequence of emergence. Details will be published elsewhere.

The nets used for the chironomid study were of simpler design. The funnel part is of rigid construction, originally built for rotary traps, with the base of the pyramid being one square meter. The much shorter sleeves have an elastic collar by which they are attached to the pyramid. Although there were virtually thousands upon thousands of chironomids flying around these nets, and many were even resting on the screen wire of the funnel, very few individuals came into the sleeve except with the wind. In calm weather and, except for the hours of the flight to shore, hardly any individuals were caught; but on one windy evening, 3979 individuals were caught in 2 double nets as shown in Figure 2. Another evening, 1430 animals were caught in a single net during one 15-minute interval; in other words, there arrived an average of 1.6 individuals each second per square meter.

FIG. 2. Stationary nets used for catching windborne chironomids.

It seems, from the experience obtained with these stationary nets, that they may be effective tools for sampling windborne and migrating insects with the satisfactory exclusion of random flying individuals. Thus they fulfill the purpose for which they were designed.

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# CARDIAC RESPONSE TO COLD OF TWO SPECIES OF MAMMALIAN HIBERNATORS[1]

This study compares the effects of cooling two species of mammalian hibernators with the effects of cooling white rats. The hibernators were 4 male golden hamsters (mean weight 110g), 4 female golden hamsters (mean weight 82g), 4 13-lined ground squirrels (mean weight 143g). The 4 male albino rats (Holtzman) used for comparison were much heavier (mean weight 505g). All animals were maintained prior to the experiment for at least one month in constant-temperature rooms, with a controlled 24-hour light cycle (12 hours light, 12 hours darkness). The tests were run in June and July. The animals were not acclimatized to cold.

## Method

Each cooling test was run once and without prior training of the animal. The procedure was to place the animal in a restraining cage (limb movements and twisting still permitted), insert 2 wound clips in the skin of the back, and attach these to the EKG leads. A rectal thermistor was then inserted and the animal allowed to rest. When the animal was completely quiet, electrocardiograms and core temperatures were taken, to be used as normal. The animal was gently moved a few feet into the cold box, and regular recordings were made over a period of about 4 hours. The cold box, maintained at 3.5° ± 0.5°C, was of 50 cubic feet capacity with a fresh air inlet. The electrocardiograph (Burdick Company) was run every 15 minutes until one minute of record free of skeletal muscle potentials was obtained. To avoid too complicated a presentation of the data, ranges of heart rates obtained from animal to animal are not shown except with the data for male and female hamsters. The Tele-thermometer (Yellow Springs Instrument Company) was read to the nearest 0.01°C; the same thermistor was used throughout the study. In a few cases where the core temperatures were not read exactly when heart rates were taken, interpolated temperatures were used.

## Results

The initial response of the rats to cold was an increase in heart rate of about 30%. Control studies showed that this was due to the cold stimulus. Only one hamster and one ground squirrel showed this same effect (Figure 1). The heart rates of the hibernators leveled off at a core temperature of about 10°C. The rate in the hamster dropped to about 18 beats per minute, while that of the ground squirrel decreased to about 10 beats per minute (Figure 2). The rats, however, showed a continuous drop in heart rate and, if it decreased to 12 beats per minute or less, the heart beat ceased. The critical point for these rats appeared to be between 13 and 15 beats per minute; two rats which were removed from cold just before reaching this point did recover. The rats which died did not show cardiac fibrillation, results consistent with those of Willard and Horvath (1959) and Kayser (1958). All ground squirrels and hamsters showed permanent recovery from this hypothermia treatment. Heart rates of female hamsters dropped slightly faster than those of the males, probably because the females were smaller (Figure 3). The tolerance time (to cardiac failure) for the rats varied from 4.0 to 5.5 hours, and the leveling off point for the hibernators varied from 3.0 to 4.6 hours.

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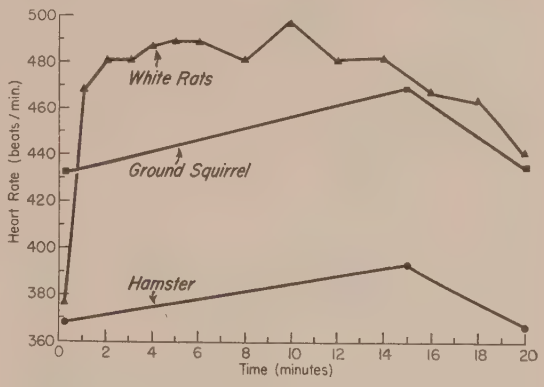


FIG. 1. Initial effects of cold exposure (3.5° ± 0.5°C) on heart rate. On white rat graph each point is a mean of 4; only one hamster (*Mesocricetus auratus*) and one ground squirrel (*Citellus tridecemlineatus*) showed the initial increase in heart rate.

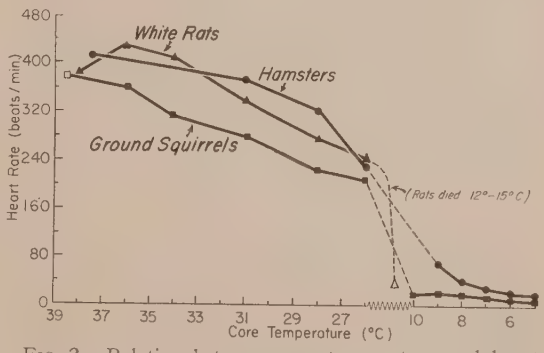


FIG. 2. Relation between core temperature and heart rate in hypothermia induced by partial restraint (ambient 3.5° ± 0.5°C). Solid points are mean of 4 readings; unfilled points are mean of 2 readings.

## Discussion

Adolph and Richmond (1956) found that the ground squirrel has the greatest resistance to the effects of cooling, followed by the hamster; the rat was least resistant. Our results showed that the heart rate of the hamster leveled off at a higher rate than that of the ground squirrel indicating that by these criteria the hamster was more resistant to cooling. The heart rate of the rats did not level off at all, indicating failure to adjust to cold. As for the hibernators, the hypothermia-of-restraint which they demonstrated is different from true hibernation (Popovic 1958). A conspicious difference is that the hypothermic heart beat leveled off at a higher rate than in hibernation at that same ambient temperature (Folk 1959). A current view is that hibernation usually requires physiological preparation (Strumwasser 1959). Therefore, it was anticipated that unprepared hibernators might not tolerate hypothermia. Instead they proved completely resistant to harmful effects of a marked reduction in body temperature.

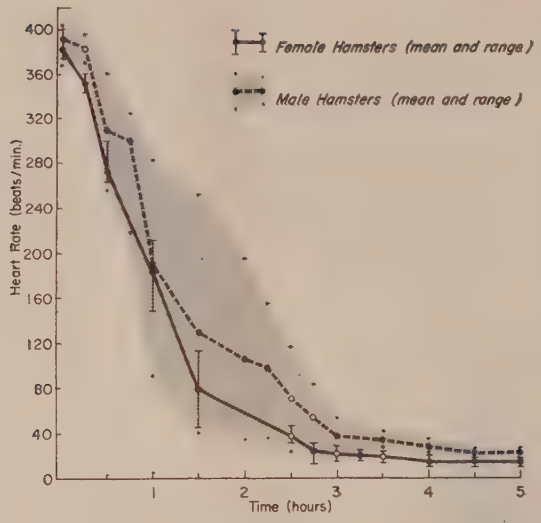


FIG. 3. Rate of reduction of heart beat in cooled hamsters (ambient 3.5° ± 0.5°C). Solid points represent mean of 4 readings; unfilled points are mean of 2 readings; the range of values about each mean is indicated.

SUMMARY

Heart rate and core-temperature relationships in cold-exposure were studied using white rats and two species of mammalian hibernators. The hearts of the rats ceased beating at a core-temperature of 12-15°C. It was anticipated that since the 13-lined ground squirrels and golden hamsters were not preconditioned by cold or by deep artificial hibernation. Instead they proved re- artificial seasonal changes, they also might not tolerate sistant to the effects of cold which were fatal to the white rats.

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## NOTES ON HOMING AND MIGRATORY BEHAVIOR OF BATS[1]

While the existence of a homing ability in bats has been demonstrated in many experiments reviewed by Cockrum (1956) and Griffin (1958), it is only recently that Cockrum (1956) and Mueller and Emlen (1957) have shown that some bats return rapidly enough to demonstrate an almost direct flight home. Yet most homing experiments have failed to show a high percentage of returns at speeds sufficient to establish the fact of accurate homeward orientation rather than wandering or exploration until familiar territory is reached. (For discussion of the theoretical problems involved see Griffin 1952a or Matthews 1955). We therefore attempted recently to obtain an improved measurement of the maximum homing performance of *Myotis lucifugus* and *Eptesicus fuscus* by timing the returns of bats released at 5 to 54 miles from summer breeding colonies or hibernation quarters in caves. Since we were interested primarily in the more rapid homers, we confined our attention to those bats that returned within 2 days; but many additional returns were also secured one to 8 weeks after release, as in several previous homing experiments. The results contribute only modestly to our general knowledge of homing in bats, but they help to explain the variability of homing performance recorded by current methods, and some interesting instances of migratory flights and group coherence were observed.

METHODS

At caves we captured returning bats with mist nets or hand nets. At summer colonies in buildings, hand nets and bat traps of the type described by Griffin (1940a) were supplemented in most cases by radioactive tagging, a method previously employed with interesting results by Punt and van Nieuwenhoven (1957). We could locate returns during the daytime at distances up to one meter even when the bats were deeply hidden in crevices.

The best radioactive tag for experiments of this type is one detectable at the greatest practicable distance from the marked animal, and yet having a sufficiently small amount of radioactivity that the animal is not injured (Griffin 1952b, Pendleton 1956). This is most simply accomplished by using an isotope of short half-life in order that the radioactivity may decay soon after the end of the experiment. Since bats had to be detected through the structure of buildings, we required an isotope emitting gamma radiation; we chose $Iodine_{131}$ because of its ready availability and its half-life of about 8 days. Special bands patterned after the German type described by Hitchcock (1957) were constructed with a flange which could be folded back against the main

[1] These experiments were supported by the Biology Branch of the Office of Naval Research. Reproduction of this paper in whole or in part is permitted for any purpose of the United States government.

body of the band. A small drop of a solution containing about 5 microcuries of $I_{131}$ was allowed to evaporate in the fold of metal and the escape of the dried material was prevented by the application of a quick-drying glue. The metal was then crimped together over the radioactive material. Such a tag was harmless to an animal carrying it for the entire lifetime of the isotope. A radioactive tag does not specifically mark an individual animal but we found in practice that several bats could be distinguished after returning to a single building because they were located in different spots, even though all were quite invisible in crevices.

## Experiments

### *Eptesicus fuscus*

In 1957 4 pregnant females were released early in the evenings of May 8 and 9 fifteen miles east of a nursery colony in Concord, Mass. Three of the 4 had returned to this colony by the following morning. But on June 4 another female from this colony, in a much more advanced state of pregnancy, failed to return during the same night it was released 15 miles east. On July 16, 1958 thirteen nursing females from this colony were released 54 miles to the south, but none was detected the next day or the day following. Twenty-eight *Eptesicus* were taken from another colony in North Westport, Mass. and released 15 miles away on the evenings of July 18, 19, and 20, 1958. Only one return was recorded the day following release, and only 5 more the second day after release. These 5 were then carried to the same release point, and on the following day 3 of them were once more back at their home colony. These observations suggest that more rapid homing may be expected early in the summer, and that a superior homing performance may be expected from *Eptesicus* which have returned rapidly from a homing experiment and are taken again to the same release point.

### *Myotis lucifugus*

In an exploratory experiment on November 20, 1955 thirty-six bats of this species were taken from a population of 100 at a cave near Plymouth Union, Vermont and were released in a small abandoned mine tunnel 5 miles south of the cave. When both cave and mine tunnel were carefully searched 5 days later after moderately cold weather 27 of the 36 bats were still in the mine tunnel. Having been released in a place suitable for hibernation, these bats, like others observed by Twente (1955a), had remained at the release point. Of the 9 bats *not* recovered where released, 3 were back at the cave after a homing flight of 5 miles in 5 days under winter conditions.

Stimulated by Mueller and Emlen's report of rapid homing of this species to a cave during the fall, we carried out 2 homing experiments on Sept. 28 and Oct. 18, 1957, using bats from the large colony in the Chester, Mass. emery mine. These bats were marked on the wings with ordinary U. S. Fish and Wildlife Service bands and were recaptured with a mist net at the entrance to the mine tunnel. They were all carried to the east, and released between 8:30 and 12:00 p.m. The weather conditions were favorable (warm and clear) on the night of September 28, but it was cool and rainy on the night of October 18, and all returning bats were quite wet when captured. The cave entrance was covered by a net on the nights of Sept. 28-29, Oct. 18-19, and Oct. 19-20. The results are summarized in Table I.

Since the Chester emery mine is located in a distinct valley, the speeds and percentages of returns could be explained on the assumption that these bats had acquired a familiarity with the topography within a radius of 10 or 20 miles and homed from greater distances by wandering or exploration. Other factors than inability to navigate over long distances could also explain these results, however, and one such consideration will be discussed below.

Table I. Results of homing experiments with *Myotis lucifugus* from mine tunnel at Chester, Mass. 1957.

| Date | Distance (miles) | Number of bats | Number of returns during first night | Elapsed time | Number of additional returns during second night |
|---|---|---|---|---|---|
| Sept. 28 | 10 | 10 | 5 | $2^h$ to $3^h45'$ | — |
| " " | 30 | 10 | 1 | $4^h25'$ | — |
| " " | 50 | 10 | 0 | — | — |
| Oct. 18 | 10 | 100 | 8 | $7^h30'$ to $9^h30'$ | 39 |
| " " | 30 | 100 | 2 | $6^h30'$ to $9^h$ | 20 |
| " " | 50 | 135 | 0 | — | 4 |

During the summers of 1957 and 1958, sixteen small groups of *Myotis lucifugus* from several different nursery colonies in southeastern Massachusetts were released at distances from 5 to 50 miles. All were released before midnight, and the roosts were carefully checked the following day, and also, in most cases, the second day after release. The results, summarized in the Table II, were quite variable—ranging from no returns in 2 nights from 10 miles to 11 out of 70 returning the same night released at 15 miles. The homing from 10 miles was surprisingly poor compared to the results from 5, 15, and 20 miles. Matthews (1955) has suggested that there is an intermediate range of distances at which homing birds can neither find familiar landmarks nor sufficiently distinct cues related to their geographical position. It is tempting to explain the present data by postulating that at 5 miles the bats were in familiar territory, while at 15 or 20 miles some sort of direct homeward orientation (type III of Griffin 1952a) became possible. But many more data would be necessary to provide an adequate test of this speculative hypothesis.

Table II. Results of homing experiments with *Myotis lucifugus* from summer colonies, 1957 and 1958.

| Distance transported (miles) | Number of releases | Number of bats | Per cent returns 1st night | Per cent additional returns 2nd night |
|---|---|---|---|---|
| 5 | 3 | 8 | 50 | — |
| 10 | 5 | 48 | 0 | 6 |
| 15 | 1 | 5 | 20 | — |
| 15 | 2 | 226 | 10 | 9 |
| 17.5 | 1 | 10 | 0 | 0 |
| 20 | 1 | 5 | 40 | — |
| 20 | 1 | 5 | 20 | 40 |
| 30 | 1 | 12 | 0 | — |
| 50 | 1 | 25 | 0 | 8 |

While the average performance registered in these homing experiments was not impressive, several isolated cases strongly suggested an ability for rapid and direct homing. For example two groups of 25 bats each were released at 5 miles from home between 4:30 and 5:30 A.M.—within ½ hour of the normal time of return to the roost in the morning. One of these bats was found

at the home roost one hour after release, and 19 more were back the following day.

It is a common observation of bat banders that when a summer colony is disturbed, as by banding most of its members, the majority may leave the colony at least for several days. For example, a female with young was banded on July 11, 1957 at a nursery colony in Dartmouth, Mass., designated building B, and was immediately released in the same building. The next day she and her young were retaken at nursery colony A, a mile away. This partly explains the anomalous results of earlier homing experiments in which a larger fraction of the bats released at a distance were recovered at the home roost than was the case if they were released locally (Griffin 1940a).

We also observed one striking example of bats returning to the general vicinity of their place of capture but roosting in another colony nearby. Twente (1955a, 1955b) has reported similar observations. In one of the homing experiments in Table II, 156 females were released between 11 and 12 P.M. fifteen miles north of colony A where they had just been captured. The following day 11 were retaken at building A, but 10 more (not included in Table II) were found in nursery colony B, situated one mile to the east. The 2nd day after the homing experiment 16 new returns were found at A together with 3 which had been at building B the previous day. Furthermore building B now contained 3 new returns and 2 bats which had moved there from building A during the second night after the homing experiments.

These demonstrated cases of shifting from one colony to another led to a careful search for nursery colonies within a radius of 10 miles of building A, and 19 such colonies have been located ranging in population from several bats to several hundred. Obviously the bats which return to a home area do not all choose the same daytime roost where they were found by the experimenter. This may also be true at caves, especially in view of the fact that in many areas such as in New England only a fraction of the population hibernate in sizeable caves where they can be seen and collected (Griffin 1945). It should also be pointed out in this connection that, in Holland, Punt and van Nieuwenhoven (1957) found that many radioactively tagged bats could be located deep in crevices of caves, either after local release or after homing experiments, in places where they would certainly have escaped detection by visual search. In short, present methods are probably inadequate to measure accurately the homing performance of bats, except under fortuitously favorable conditions where a large proportion return to the place where they were captured rather than to some alternative daytime roost.

*Migratory flight and group coherence*

In the course of these homing experiments the following incidental observations added significantly to the few recorded recaptures of banded bats relatively soon after long migratory flights. On Sept. 28, 1957, twenty-six female *Myotis lucifugus* were banded and released close to the Chester emery mine where they had been caught along with the animals used for the homing experiment described above. During the following June, 11 of these females were retaken among approximately 200 others of the same species at nursery colony A in Dartmouth, Mass. These bats had migrated a minimum distance of 112 miles southeast and all were found in one nursery colony but none at any of several others nearby. Evidently these animals belonged to a group which tended to remain together (for other evidence of group coherence see Griffin 1940b). On November 29, 1958 another of these 26 females banded at Chester (not one of the 11 retaken at Dartmouth in June) was recaptured in a cave on Mt. Aeolus, East Dorset, Vermont, 65 miles north of Chester. This cave has previously been noted for a transient fall population (Griffin 1940a).

One of a group of 70 females captured August 10, 1958 at nursery colony B in Dartmouth, Mass. was also retaken at East Dorset, Vermont on November 29, 1958. It was one of the 11 which had returned to its "home" roost at Dartmouth on the first night after release 15 miles distance. Its migration to the cave in Vermont required a minimum flight of 155 miles northwest in 110 days.

## Summary

1. Homing experiments with *Myotis lucifugus* and *Eptesicus fuscus,* some marked by radioactive tags, showed a highly variable homing performance during the first 2 nights after release. In some cases no returns were detected even at distances as short as 10 miles. In other experiments as many as 75% of the *Eptesicus* returned in the first night from 15 miles. Up to 60% of the *Myotis* returned from 5 miles, up to 40% from 20 miles, and as many as 10% from 30 miles during the same night that they had been transported and released.

2. Homing bats often return to the general area where they were captured initially, but choose a different building as a daytime roost. This was demonstrated in one case, and is strongly suspected to be the usual occurrence. This complicates the interpretation of homing experiments with bats, and demonstrates the need for improved methods for studying homeward orientation in these animals.

3. Three migratory flights were detected by recapture of banded bats; in one case 11 out of 26 female *Myotis lucifugus* banded at a cave in September 1957 were recovered in one of several nursery colonies examined 112 miles to the southeast during the following June. Another of these 26 females was retaken in November 1958 at a cave 65 miles north of the original place of banding. A 3rd female *Myotis lucifugus* banded in August at a nursery colony in southeastern Massachusetts was retaken 110 days later 155 miles northwest at a cave in Vermont.

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## PENETRATION OF FRESH WATER THROUGH TWO OCEANIC STREAM BARS

The homing of anadromous fishes has been presumed to be chemically influenced by the specific constituents of parent streams. However, the ability of some species to "home" in the apparent absence of an available home stream stimulus has been noted by various authors (see Hasler 1956, also Shapovalov and Taft 1954). The presence of fish off the entrance of a stream with the ocean bar intact has suggested that other mechanisms might be involved.

An investigation was made to determine whether chemical differences might exist off the oceanic bars of 2 previously studied streams such that the gathering of steelhead and salmon could be accounted for by these differences. These bars were closures of 2 streams previously studied as to fish activities by Shapovalov and Taft. The major stream was Waddell Creek in Santa Cruz County, California (lat. 37° 6′ N, long. 122° 17′ W) and a smaller stream, Scott Creek, about 5 miles southeast.

Both streams are subject to reduced flow in summer. At these times, the sand barrier at the terminus completely blocks surface flow and a lagoon of fresh or brackish water is backed behind this. Scott Creek may cease all flow in dry summers but Waddell Creek continues to provide a lagoon at all times. As the fall rains increase stream flow, the lagoons increase and may, especially after a storm, break through the barrier. However, in most years the bar does not remain breeched on this first occasion but reseals. Permanent opening dates vary over several months.

Water samples were obtained at both bars. These were checked for specific gravity by the use of a Westphal balance but the results were so exceptional that confirmation was made with silver nitrate titration. The conversion of these titration figures to salinity was based on the formula of Lyman and Fleming (1940). $\Sigma\,{}^{o}/_{oo} = 0.073 + 1.8110\mathrm{Cl}\,{}^{o}/_{oo}$.

The point of significance was that at Scott Creek, the seepage through the bar was sufficient to provide an actual local difference in the salinity of the sea itself. Waves sampled in the vicinity of the bar gave a salinity of 33.07 ${}^{o}/_{oo}$ while samples of the waves taken upwind (upcurrent) gave 36.60 ${}^{o}/_{oo}$ (Nov., 1958), Waddell Creek at this same date had seepage waters flowing out of the bar at low tide with a salinity of 26.39 ${}^{o}/_{oo}$.

It would appear that it is not necessary to postulate "guideposts other than odor" as Hasler claimed on the basis of the work of Shapovalov and Taft. Long before the bar breaks, there must certainly be plenty of chemical influence in the adjoining sea such that the concentration of fish in preparation for the opening is explainable on this basis.

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## NOTES ON THE HARVESTER ANT, *POGONOMYRMEX BARBATUS* VAR. *MOLEFACIEUS*, IN SOUTH TEXAS[1]

Although early workers (McCook, 1897) recognized the importance of the harvester ant in Texas agriculture and studied its life history in detail, little is known about its occurrence, density, and ecological relations on native rangelands.

During an intensive South Texas study of plant-soil relationships (Box 1959) mounds of the Texas harvester ant were recorded on 25 one-tenth acre quadrats on a prickly pear-short grass community, a chaparral-bristlegrass community, a mesquite-buffalo grass community, and a bunchgrass-annual forb community. The mesquite and chaparral communities occurred on Victoria clay, the bunchgrass community on Nueces fine sand, and the prickly pear community on Orelia clay loam. Ants were present in all communities, but in most cases they were found in such low numbers that it was impossible reliably to estimate their densities with the sampling method employed. However, data showed that the prickly pear-

[1] Contribution number 39, Series A. from Welder Wildlife Foundation, Sinton, Texas.

short grass community averaged 8.4 mounds per acre with fiducial limits at the .05 level of 5.1 to 11.7 per acre.

The average mound occupied 15.3 square feet and a total of 128.7 square feet per acre was denuded by ants. Mounds usually had from one to 3 openings near the center of a bare area ranging from 2 to 7 feet in diameter. The outer portion of the cleared tract was surrounded by a ring of annual 3-awn grasses (*Aristida oligantha*). From 2 to 8 foraging trails led from the cleared space into the vegetation of the surrounding region. The immediate area around the mound contained seeds of several plant species.

Soil from 15 randomly located square-inch quadrats was removed to a depth of ¼ inch in the cleared openings at each of 5 ant mounds. A total of 656 seeds was found in the 75 samples examined giving an average of 8.7 seeds per quadrat. Seeds from prickly pear (*Opuntia lindheimeri*), agarito (*Berberis trifoliata*), and 9 grasses were found (Table I). Seeds of plains bristlegrass (*Setaria macrostachya*), 3-awn grasses, and buffalo grass (*Buchloe dactyloides*) comprised more than ½ of the grass seed present.

TABLE I. Comparison of numbers and percentages of plant seeds found in the cleared areas around Harvester ant dens on the Welder Wildlife Refuge, in South Texas.

| Species | Seeds per square inch | Percentage of total seeds | Percent composition of plants on area |
|---|---|---|---|
| Opuntia lindheimeri | 3.6 | 41.1 | 22.3 |
| Berberis trifoliata | 2.0 | 4.5 | 2.6 |
| Sporobolus pyramidatus | 0.1 | 0.6 | 5.1 |
| Setaria macrostachya | 1.7 | 19.4 | 8.3 |
| Eragrostis sp. | 0.1 | 0.4 | Trace |
| Buchloe dactyloides | 1.0 | 11.0 | 14.3 |
| Aristida sp. | 1.2 | 13.1 | 8.3 |
| Panicum filipes | 0.2 | 2.6 | 0.7 |
| Andropogon saccharoides | 0.1 | 0.4 | 5.8 |
| Cenchrus sp. | 0.4 | 4.4 | 5.8 |
| Hilaria belangeri | 0.1 | 0.9 | 21.1 |
| Unknown | 0.1 | 1.2 | — |

On August 6, 1958, 5 ant mounds were studied for a 24 hour period. Numbers of ants entering each den were counted for 3 minutes at 2 hour intervals. Temperature of the soil surface was taken during each counting period. The relationship between ant activity and soil surface temperature is shown in Figure 1. Greatest ant activity was reached at 10:00 P.M. when the soil surface temperature was at its lowest. Virtually no activity was recorded between 12:00 noon and 4:00 P.M. During this period soil surface temperatures were greater than 130° F and the few ants that ventured from the den never went more than a few inches from the opening. Mangrum (1954) reported that stupor appeared in *Pogonomyrmex barbatus* var. *molefacieus* at temperatures between 115 and 122° F and this appeared to be true of the ants in the present study. The relationship between ants entering their dens and soil surface temperatures exhibited a highly significantly negative correlation of — .877.

Seldom was an ant seen on the trails leading from the

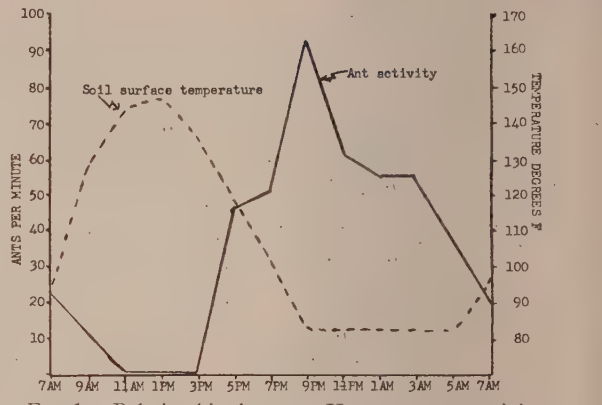


FIG. 1. Relationship between Harvester ant activity and soil surface temperature for a 24 hour period.

mounds between 4:00 P.M. and 9:45 P.M. Most of the ant activity during the early part of the night was within a few inches of the opening and consisted mainly of removing seeds from the den. About 90% of the seeds removed were those of prickly pear which had been thoroughly cleaned of all the fleshy fruit. Around 10:00 P.M. the ants began using their foraging trails. From that time until about 5:00 A.M. large amounts of food were carried into the dens. This food was mainly prickly pear seeds with bits of the tuna attached. Activity ceased on all trails by 5:45 A.M. and work was restricted to carrying cleaned prickly pear seeds from the dens. As soil temperatures increased, the ants withdrew into their dens and did not reappear until late the next afternoon.

An estimated number of 1483 seeds per square foot was calculated from samples taken within the cleared areas surrounding the mounds, or an average of 22,689 seeds per ant den. These seeds were largely discards and did not represent those removed and used as food. The removal of the large amounts of grass seeds and the deposition of prickly pear seeds may have a profound effect on future vegetational composition of the plant community. However, the place of the harvester ant in the over all ecology of natural communities has not been studied sufficiently to isolate their effects on native ranges.

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## AN OCCURRENCE OF "CHIMNEY" CONSTRUCTION BY THE CRAYFISH *CAMBARUS B. BARTONI*

Burrowing by the crayfish *Cambarus bartoni bartoni* has not been reported from New York (Crocker 1957) but Ortmann (1906) had often found the burrows of this crayfish in Pennsylvania.

On Sept. 8, 1959, while collecting crayfish in Catatonk Creek at Candor, Tioga County, N. Y., I noticed many obvious "chimneys" in an area of stony rubble which extended along the creek for about 90 meters (Figure 1).

FIG. 1. The exposed rubble area where "chimney" formations were numerous.

This area would probably be inundated through much of the year but was exposed at the time of observation as the creek was at a low level. The "chimneys" were very numerous, often being less than a foot apart. They extended from the stream back through the rubble for 2.5 to 4.0 meters to where the land was slightly higher and grasses and tall pasture weeds occurred.

Ortmann (*op. cit.*) did not credit *C. b. bartoni* with constructing a very neat "chimney" but said that "its more or less regular mounds often assumed the shape of 'chimneys.'" He also remarked, however, that even with obligate burrowers, regular "chimneys" are scarce and that most are more or less irregular and shapeless mud piles. Most of the stuctures observed at this time appeared to be very distinct "chimneys" (Figure 2) with the exception that many were only semicircles. In this latter situation, the crayfish had worked up from under a stone and had deposited the excavated material as a semicircular wall adjoining the stone (Figure 3). Some "chimneys" were "plugged" and appeared as cone shaped mounds. Many were moist, indicative of current activity. They ranged considerably in size, the largest circular "chimney" having an outside diameter of 8 cm. One rectangular wall adjoining a stone had outside measurements of 4 x 15 cm (Fig. 3). A male of 25.5 mm carapace length was later taken from this burrow.

The area was visited at night, but no activity was seen. The area was then revisited by day and some of the burrows were opened. Ten *C. b. bartoni* ranging from 12.9 to 28.1 mm carapace length, were thus obtained from individual burrows. One was a soft male II that had just molted, its exuvia I still being present. In one large burrow occupied by an adult male I, an advanced larva was also present.

Francois (1959) noted that the burrows of *C. b. bartoni* within the stream were quite elaborate at times. This also seemed to be the case here in the exposed rubble area. Some burrows appeared to consist merely of hollows under stones, but in many cases lateral passageways seemed to exist in the rubbles. The burrows could not be followed readily as slowly moving water was present just a few inches below the surface. Thus, as fast as a stone was removed, the hole flooded with muddy water. All the occupied burrows appeared to be quite shallow, none being deeper than 10 cm. At that depth a distinct flow of water through the rubble was noticeable.

FIG. 2. Two adjacent "chimneys" that are typical of the structures observed in the area. The "chimney" at the right is seen in side view.

FIG. 3. A non-circular "chimney" adjoining a stone. Most structures of this kind were semicircles, but this one tended to be rectangular.

Another exposed rubble bed about 3 miles upstream was examined and there too many "chimneys" were seen.

The original area was visited once again by the author accompanied by H. Gray Merrian who took the photographs accompanying this note.

Ortmann (*op. cit.*) observed *C. b. bartoni* burrows in stream banks and on one occasion, even in a swampy

headwaters area. He made, however, no mention of burrowing under conditions similar to those reported here. Ortmann believed that *C. b. bartoni* only burrowed when forced to by the lowering of the water table, and he observed burrows that were 45 cm deep.

In the situation reported here, the creek was still at good flow (Fig. 1) and, although *C. b. bartoni* was common in the stream, many stones therein did not shelter any crayfish. It seemed interesting therefore that the crayfish in the rubble had burrowed and constructed "chimneys" instead of moving a short distance into the stream proper. The same burrowing activity probably also occurs in the stream where the overflowing water prevents the formation of the "chimney." Mounds of sand and pebbles lying adjacent to undermined stones were observed in the stream bed next to the rubble area. Francois (*op. cit.*) mentions observing similar mounds by the burrows of *C. b. bartoni* in New Jersey streams. These mounds, however, are probably of short duration. In view of the similarity of the burrowing activities observed at Catatonk Creek, it is suggested that "chimney" construction by *C. b. bartoni* is not a unique activity and is basically no different from this crayfish's usual burrowing activity within a stream.


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## VARIATIONS IN SIZE OF OSTRACODS CULTURED FROM DRIED SOIL IN THE LABORATORY

In describing new species of ostracods, G. O. Sars made much use of cultures from dried mud from different parts of the world. The descriptions he made, of course, included measurements of size for the various species. Size has always been a strong descriptive feature among ostracod taxonomists. In the ostracod literature, it is not difficult to find new species established on the basis of size difference, sometimes in addition to one or more other minute, inconsequential differences. In culturing ostracods from soil removed from evaporated pond areas, I have observed that ostracods cultured in the laboratory may be different in size from ostracods of the same species observed in nature.

In documenting the correctness of these observations, measurements were made on 20 gravid females of one species of ostracod randomly collected from a vernal pond in the Spring of 1958 as the pond was nearing the time of complete evaporation. Later, measurements were made on 20 gravid females of the same species taken from cultures of soil from the same pond area after desiccation.

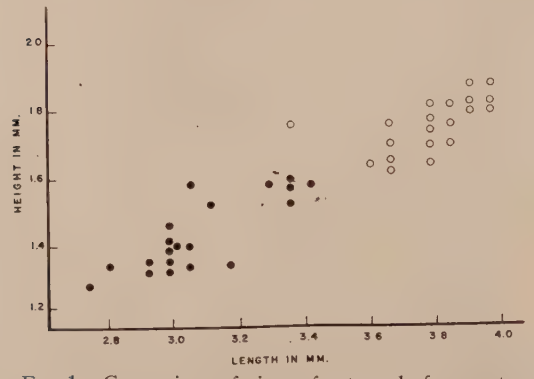


Fig. 1. Comparison of sizes of ostracods from nature and ostracods cultured from dried soil in the laboratory. Solid circles represent individuals cultured in the laboratory; open circles represent individuals from the natural environment.

The average of the lengths of the individuals taken from the natural situation was 3.79 mm; the average of the heights was 1.77 mm. On the other hand, the average lengths of the individuals taken from the laboratory culture was 3.08 mm; the average of the heights was 1.44 mm. On the accompanying graph, lengths of the individuals taken from the 2 situations are plotted against their heights. It will be seen that most of the individuals from the natural environment were larger than those cultured in the laboratory. In addition, a greater degree of variation may be indicated for the individuals from the laboratory culture. This evidence throws doubt on the reliability of new species described from laboratory-cultured material and on use of size as a criterion in establishing new ostracod species, unless, of course, a considerable size difference is involved, and the difference is supported by other definite physical or physiological differences.


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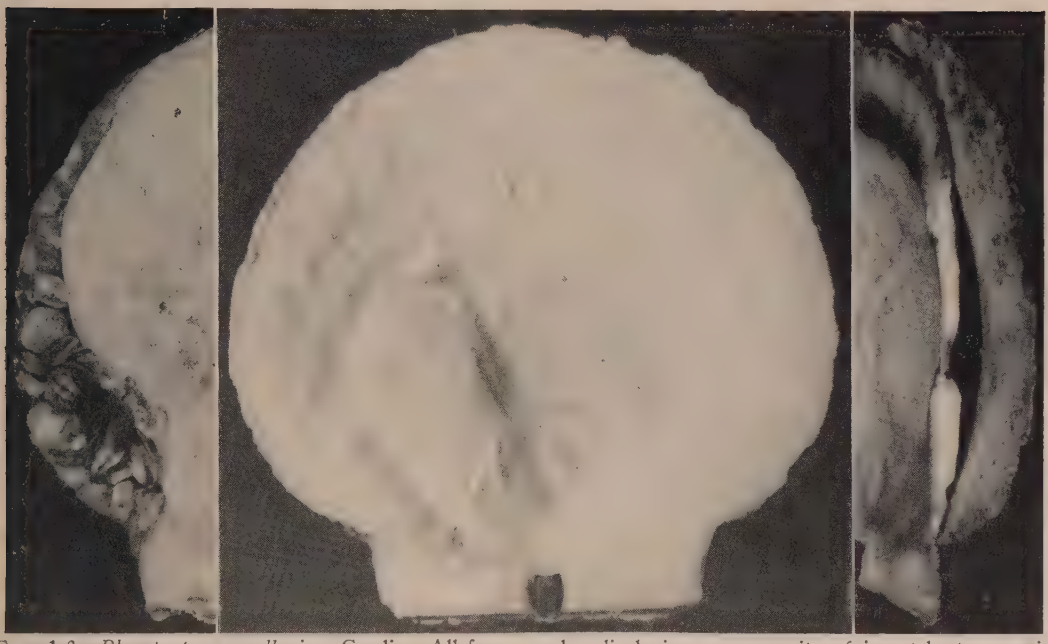
# LIVING INCLUSIONS IN THE SHELL OF THE SEA SCALLOP *PLACOPECTEN MAGELLANICUS*[1]



FIGS. 1-3. *Placopecten magellanicus* Gmelin. All from Cape Cod Bay, Massachusetts (about N. Lat. 41° 47′, W. Long. 70° 20′).

1. (center)—Interior view of left valve to show coating of new shell over mud-sand debris.

2. (left)—Interior view of an anterior portion of left valve displaying a community of invertebrate organisms within the periphery of the shell of the scallop.

3.—Oblique view of interior of posterior edge of right valve to reveal new shell material slowly being added toward margin.

A curious deformity of the shell is observed infrequently in the sea scallop *Placopecten magellanicus* (Gmelin). It occurs when foreign matter becomes lodged between the mantle and the shell. Unable to expel the material the animal secretes over it a protective barrier which prevents further injury or irritation (Figure 1).

An elaboration of this condition occurs when an excessive amount of foreign substance forces a portion of the mantle inward from its normal position along the margin of the shell. A protective barrier is secreted as usual but because of the awkward position of the mantle the new shell lining cannot reach the rim of the shell. Larval organisms are quick to take advantage of the scallop's predicament. They settle in the convenient niche within the protective lip of the shell and thrive in the currents created by the feeding of the scallop. The sensitive mantle margin of the scallop meanwhile begins to secrete a partition at the point of contact with the trespassers which prevents further invasion (Figure 2). If the scallop is later able to extend its mantle nearer the shell edge (Figure 3) it may cover or crowd out the fouling organisms, eventually reaching the border and ridding itself of the last of the intruders.

I have seen several examples illustrating various stages of the above condition. It is probably caused in many instances by the action of the scallop dredge used by commercial vessels as it scrapes up mud and sand along with the scallops. Often some of this mixture is forced between the valves and behind the mantle which, if the scallop escapes, occasionally creates the situation described above.

The method of repair is as follows. First the surface of the mantle membrane secretes a thick layer of dark organic substance similar in appearance to the "tanned proteins" of which the ligament in *Pecten* is constructed (see Trueman 1953). This organic product of the mantle is commonly referred to as conchiolin. Droplets resembling nacre[2] are deposited over the conchiolin usually starting the edge and working inwards but at times more or less at random. In this manner a foundation is quickly produced on which thin layers of "nacre" are then laid to create a thin crust. Areas in the crust frequently break causing an additional deposition of the organic matrix by the mantle surface over which more "nacre" is deposited. As layer after layer builds up the crust thickens. After the lining becomes substantial and the animal is protected, any slight depressions and rough spots are filled in until the inner shell surface is again relatively smooth.

The whole process of initial repair in the less serious cases is a matter of a short period of time, possibly only days. This can be ascertained by studying the edge of scallop shells that have undergone this type of repair. When a scallop has been disturbed a distinct

[1] The author is indebted to Colonel Eugene S. Clark, Jr. for securing specimens of the sea scallop which exhibited living inclusions, and to Captain Richard Mayhew of the scallop vessel *Charlotte* who helped collect a series of deformed shells for further study.

[2] Nacre or mother-of-pearl always consists of aragonite. In the *Pectinidae* the inner layer of calcium carbonate is crystallized in the calcitic form (Böggild 1930).

check forms at the edge and new growth can be recognized. New growth is apparent in recaptured tagged scallops after as short a period as 3 weeks.

Parker (1932) reported on a specimen of *Mya* in which a rhizome of *Spartina* had penetrated between the shell and mantle. Utilizing the winter growth-lines he was able to remark on the vigorous and active processes of recontruction to produce in a relatively short time a thick covering crust over the rhizome.

The organisms seen in the shell in Figure 2 are typical of those which are usually found in this situation in Cape Cod Bay, Massachusetts. Three species of bivalve mollusks made up the greater part of the inclusions.

| *Species* | *No. of specimens* | *Size range (mm)* |
|---|---|---|
| *Mytilus edulis* Linné | 30 | 0.3-14.6 |
| *Hiatella arctica* (Linné) | 28 | 1.1-14.8 |
| *Anomia aculeata* Gmelin | 23 | 1.5-15.0 |

Other invertebrate intruders in the shell were an encrusting bryozoan, some branching hydroids, a single polychaete annelid (Polynoidae), and 28 tiny barnacles, *Balanus* sp., 0.5 to 1.4 mm in diameter.

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## TRANSPIRATION RATES OF ARCTIC AND ALPINE SHRUBS[1]

Within tundra regions of North America, shrubs 0.5 to 2.0 m in height are a conspicuous feature of the vegetation, although they seldom dominate except locally in protected sites as along small stream channels, lake shores and marshes, steep slopes, lee side of rocks, and along river flood plains in the Arctic. Though the shrubs are somewhat protected, their relatively large transpiration surface is in contrast to the much smaller leaf surface of the low grasses, sedges, forbs, and dwarf heath shrubs which dominate these tundra regions.

The present study was made to investigate the effect of various environmental factors on transpiration rates of different shrub species within one tundra area as well as to compare transpiration rates in arctic and alpine tundras.

### Methods

Transpiration rates were determined for 4 arctic shrub species at Umiat, Alaska (152° 10′ W, 69° 22′ N, and 350 feet above sea level). The alpine measurements were made on 2 species in the Medicine Bow Mountains of Wyoming (106° 19′ W, 41° 20′ N, and 11,000 feet elevation), and on 2 species in the Alpine Gardens on Mt. Washington, New Hampshire (71° 18′ W, 44° 16′ N, and 5,200 feet elevation).

The potometer method was used to measure transpiration. Branches were cut under water and attached to water-filled graduated pipettes with rubber tubing. Triplicate samples for each of two species were run at one time for 24 or 30 hours. The runs were made in small meadows within a few hundred feet of where the branches were collected. Two transpiration runs were made for each species, one under clear to partly cloudy conditions and the other under cloudy skies.

A continuous record of air (10 cm) and soil (−10 cm) temperature was obtained with a distance recording thermograph. Wind speed was measured with a 3-cup anemometer at 1.8 m in Alaska and 0.6 m in the alpine areas. Relative humidity was measured near the surface with a sling psychrometer, and the data converted to vapor pressure deficit (VPD) expressed in inches of mercury.

The potometers were run from noon to 18 hr the following day. Readings were made every 2 hours from 6 to 18 hr with no readings at night (18 to 6 hr). Experimental runs were not counted if the leaves were wilted or dried at the end of the 24 or 30 hours. Leaf surface was estimated at the end of each run by removing approximately 20% of the leaves per experimental branch, tracing their outline on paper and then determining leaf surface (lower only) with a planimeter. Most of the stomates were on the lower surface in all of the species. Transpiration rates are expressed in cc/dm²/period of time (per hour or total period of experiment).

### Results and Discussion

The data in Figure 1 and Table I show that in Alaska, *Betula nana* L. ssp. *exilis* (Sukatch.) Hult. transpired at a greater rate per unit leaf area than *Alnus crispa* (Ait.) Pursh. On July 12 and 13 transpiration was relatively high from 12 to 18 hr the first day, dropped off at "night" and remained at a lower level the second day. Air tem-

Table I. Transpiration rates for tundra shrubs in Alaska, Wyoming, and New Hampshire. Average total water losses in cc/dm²/30 hours based upon 3 determinations per experiment.

| Species | Dates | cc/dm²/30 hrs. | Dates | cc/dm²/30 hrs. |
|---|---|---|---|---|
| | | Alaska | | |
| *Alnus crispa* | July 12-13 | 0.254±0.009 | July 30-31 | 0.695±0.126 |
| *Betula nana exilis* | July 12-13 | 0.674±0.149 | July 30-31 | 0.906±0.253 |
| *Salix pulchra** | July 26-27 | 0.348±0.039 | August 10-11 | 0.288±0.083 |
| *Salix richardsonii** | July 26-27 | 0.249±0.097 | August 10-11 | 0.162±0.035 |
| | | Wyoming | | |
| *Salix brachycarpa* | July 12-13 | 0.214±0.017 | July 20-21 | 0.232±0.044 |
| *Salix planifolia monica* | July 12-13 | 0.413±0.067 | July 20-21 | 0.363±0.130 |
| | | New Hampshire | | |
| *Betula minor* | July 30-31 | 1.210±0.022 | August 11-12 | 1.082±0.130 |
| *Salix planifolia* | July 30-31 | 0.294±0.022 | August 11-12 | 0.693±0.226 |

* Data for 24 hours.

[1] Sincere appreciation is made to the Boston University Physical Research Laboratories, the Duke University Research Council, and the National Science Foundation Grant G 5119 for aid in supporting the field work upon which this paper is based.

perature and VPD were about the same both days while wind speed and cloud cover were greater the morning of the second day, which effectively held transpiration at a lower level. The afternoon of July 30 both temperature and VPD values were a bit higher than during the previous experiment; however, wind velocity was also greater. These stronger winds (8 mph) apparently tended to reduce transpiration although the sky was quite clear. The second day (July 31) the sky was clear, VPD and air temperatures were again high while wind speed dropped considerably; the result was a rapid rise in transpiration for both species (Fig. 1).

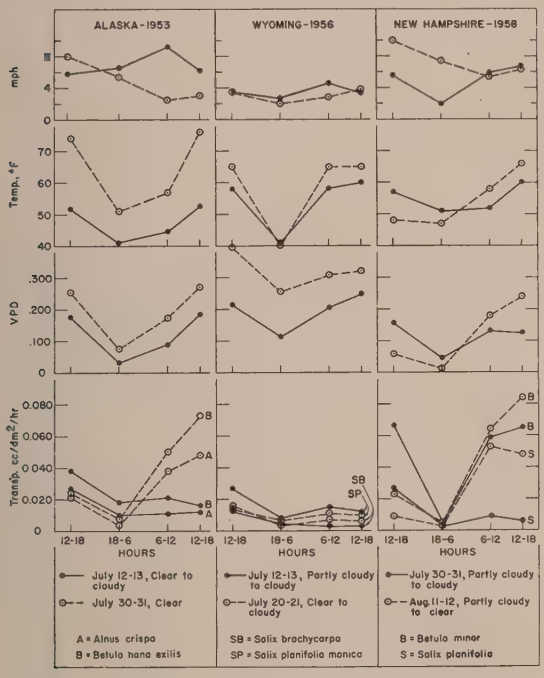


FIG. 1. Microenvironmental data including wind (mph), air temperature at 10 cm (°F), and VPD (inches of mercury) along with transpiration rates (cc/dm²/hr) for tundra shrubs in Alaska, Wyoming, and New Hampshire. All data are 6 hr averages during the daytime and 12 hr averages at night (18 to 6 hr).

Transpiration rates of *Salix pulchra* Chame. and *S. richardsonii* Hook. were considerably greater during the July 26-27 experiment than during the August 11-12 one, although environmental conditions were more conducive to high rates during the second. This probably resulted from a general reduction in physiological activity which accompanied the initiation of fall leaf coloration by mid-August. Water losses per unit leaf area were always less in the willows than in dwarf birch and *Salix richardsonii* transpired at lower levels than *S. pulchra* (Table I).

Temperature inversions and low VPD at night are common even during continuous light (Bliss 1956, Warren Wilson 1957) termed "midnight sun" provided the days are warm and clear to partly cloudy. Hourly rates measured on cloudy days were very similar to those at "night" when the sun was low in the sky as well as on nights with 2 or more hours of darkness. Curtel (1890) in Norway (62° N) using the potometer method, Stocker (1931) at Abisko (68° N in Swedish Lapland), and Dadykin (1954) in Siberia indicated reduced transpiration rates at "night." The latter two workers measured the rates of loss in weight of shoots and leaves immediately after detachment. Stocker (1931) reported transpiration rates of 0.175 cc/dm²/hr for *Vaccinium vitis idaea* L. on a clear, warm day and 0.082 cc/dm²/hr on a cloudy, cold day at Abisko. Transpiration for *Betula tortuosa* Ledeb. ranged from 0.048 to 0.295 cc/dm²/hr on a cloudy day. Values for other species ranged from 0.100 to 0.279 cc/dm²/hr.

Of interest in tundra transpiration studies is the work by Warren Wilson (1957, 1959). He found that leaf temperatures of *Salix arctica* Pall. exceeded air temperatures by 2° to 11°C on sunny days and 1° to 3°C at "night" and on cloudy days. While evaporation rates around tundra plants were closely related to wind speed, he believed that wind is more important in lowering leaf temperatures than in promoting excessive transpiration with a resultant water balance deficit within the plant.

Wulff (1902) believed that the well developed root systems of the arctic species permitted adequate water absorption and that transpiration occurred at temperatures near freezing. Dadykin (1954) stated that while low air and soil temperatures reduced plant growth and development, the cold soils are not physiologically dry, for various physiological processes including water absorption are adequate to meet the demands of transpiration.

During the present study, soil temperatures at —10 cm ranged from 36° to 43°F in Alaska, 47° to 52° in Wyoming and 51° to 54° in New Hampshire. These temperatures were comparable to those of the soil in which the intact shrubs were growing and apparently high enough to permit adequate soil water absorption.

In Wyoming, transpiration rates were higher for *Salix planifolia* Pursh var. *monica* (*Bebb.*) Schn. than for *S. brachycarpa* Nutt. during both runs (Fig. 1) but the differences were not statistically significant at the 5% level. Transpiration rates were about the same in both experiments which is in accord with the similar temperature and wind regimes, though VPD values were considerably higher during the second experiment.

The Wyoming shrub rates are low when compared with the shrubs in the other tundras (Table I) and very low in comparison with the rates given by Whitfield (1932) for Pike's Peak, Colorado. Working with potted plants of *Helianthus annuus* L. he reported transpiration rates of 2 to 3 cc/dm²/hr.

Working in the Alps, Pisek and Cartellieri (1934) reported transpiration rates for evergreen Ericaceous shrubs including *Vaccinium vitis idaea* L., *Empetrum nigrum* L., and *Loiseleuria procumbens* (L.) Desv. as being under 0.500 cc/gr fresh wt/hr. Values for summer green shrubs ranged from 0.500 to 1.000 cc/gr fresh wt/hr. Cartellieri (1940) gave rates of 0.480 to 0.969 cc/gr fresh wt/hr on a clear day and 0.300 to 0.690 cc/gr fresh wt/hr on a cloudy day for *Ranunculus glacialis* L.

In the Alpine Gardens of Mt. Washington, transpiration rates were much higher for *Betula minor* (Tucherm.) Fern. than for *Salix planifolia* Pursh. Transpiration rates were high for birch the afternoons of July 30 and 31 while water loss in *Salix planifolia* decreased the second day. The latter may be the result of "plugging" of xylem elements though no wilting occurred. During the second run in early August, transpiration was low the first day, which correlates well with low temperature and VPD plus cloudy skies and strong winds. The second day the sky cleared with a corresponding rise in temperature

and VPD and a reduction in wind speed with a resultant rapid rise in water loss.

In both Alaska and New Hampshire, birch transpiration rates per unit leaf area were considerably higher than in alder and the willows. Leaf thickness and leaf size may be important factors with regard to these higher water losses per unit leaf area. Leaves of both birch species were somewhat thicker than those of alder and the willows, thus they may have a greater internal surface area which would increase transpiration (see Turrell 1936). In general, the birch leaves were small averaging 0.75 $cm^2$ for *Betula nana exilis* and 2.0 $cm^2$ for *Betula minor*. *Alnus crispa* leaves were largest (8.4 $cm^2$) while the various species of willow ranged from 1.2 $cm^2$ in *Salix planifolia* to 3.3 $cm^2$ in *S. richardsonii*. It appears that small leaves may have higher transpiration rates per unit leaf area than larger leaves. In support of this are the higher losses for *Salix pulchra* (1.3 $cm^2$ per leaf) versus *S. richardsonii* (3.3 $cm^2$) and for the birches versus the other shrubs. A similar pattern is seen in the Wyoming willows with losses greater in *S. planifolia monica* (1.5 $cm^2$ per leaf) than in *S. brachycarpa* (1.9 $cm^2$).

While per unit leaf area transpiration rates were relatively higher for the species of birch, the small size of the shrubs with a correspondingly small total leaf area, greatly reduces losses per plant when compared with the larger willow and alder shrubs. Thus, actual differences in transpiration rates between the species may be quite minor when expressed on an entire plant basis. This is indicated by the frequent occurrence of the birch and willow species in similar habitats in Alaska and on Mt. Washington.

Differences do exist between the willow shrubs in Wyoming with regard to habitat preference and transpiration rates. *Salix planifolia monica* grows in moist to wet areas, while *S. brachycarpa* is selected out into the drier soils and wind swept upland meadows and fellfields. The latter species is much shorter, with a smaller leaf surface per plant and lower rates of water loss per unit leaf area (Table I).

A comparison of transpiration rates for the shrubs in the three tundras is difficult since different species were involved and the measurements were made under natural daily weather conditions which were highly variable. However, a few generalizations may be made.

Hourly rates of water loss at night were quite similar in the three tundras although hours of darkness varied from 2 hours in the Arctic to about 9 hours in both alpine areas. In Alaska hourly rates at "night" were somewhat higher when the sun did not set. In both the arctic and alpine tundras, hourly night rates were comparable to hourly rates on cloudy days.

With a decrease in atmospheric pressure at high altitudes, one would expect an increase in transpiration (Meyer and Anderson 1952). Water losses were greatest in the Mt. Washington shrubs while those at 11,000 feet in Wyoming gave the lowest rates. Assuming the Wyoming shrubs transpired normally, other factors must compensate for the reduction in atmospheric pressure at this altitude.

These data indicate that on a diurnal basis there is a direct relationship between transpiration rate, VPD, and air temperature, with an inverse relationship with cloud cover and wind, when wind speeds are above 6 to 8 mph. At wind speeds below 6 mph the relationship with water loss is direct. At these higher wind speeds, stomates undoubtedly close which would effectively reduce transpiration (see Meyer and Anderson 1952). In addition, the higher winds reduce both air and leaf temperature.

The rates of water loss measured here seem very low when compared with rates for temperate plants. Admittedly comparisons are difficult when such different methods of measurement are employed. Meyer and Anderson (1952) site figures of 0.5 to 2.5 $cc/dm^2/hr$ for broad leaved plants of temperate regions under conditions favorable for stomatal transpiration. Rates at night or under unfavorable soil moisture or other unfavorable conditions may fall to 0.1 $cc/dm^2/hr$ or less. The figures in the present study which range from 0.006 to 0.048 $cc/dm^2/hr$ are quite low, yet investigators in other tundra locations have also reported low rates.

While these comparative data on tundra shrub transpiration rates are of interest, they may not be comparable to data from intact plants, for the potometer method using detached branches was employed. Thus, the measured rates were based upon water absorption by stems in a free water system rather than based upon water absorption by intact roots growing in soil where moisture stress becomes an important factor. As pointed out by Meyer and Anderson (1952), transpiration rates from detached shoots do not necessarily bear a direct relationship to transpiration measured from intact shoots. However, for field work in these remote areas, the potometer method is very convenient and it is hoped that the data do show a close relationship with data from intact plants.

While winter snow pattern is of great importance in the distribution and relative height of tunda shrubs, transpiration rates which differ between species and genera may also be a limiting factor in distribution patterns as shown by the Wyoming data.

## Summary

Transpiration rates for species of willow, alder, and dwarf birch shrubs were measured by the potometer method in the arctic tundra of northern Alaska and the alpine tundras of Wyoming and New Hampshire. At the same time data were collected on air and soil temperature, vapor pressure deficit, wind, and cloud cover.

On a diurnal basis, water losses were directly related to air temperature, VPD, and wind speeds below 6 mph while inversely related to cloud cover and wind speeds above 6 to 8 mph.

Although different species were measured under different atmospheric conditions, transpiration rates per unit leaf area for the shrubs were highest in New Hampshire, lowest in Wyoming and intermediate in Alaska. In general, willow transpiration rates were lower than those for birch with alder intermediate.

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## AN ELECTRIC DENDROGRAPH[1]

A newly-designed electrically-operating dendrograph (Fig. 1) was added to the Neotoma[2] woody stem radial growth researches in April, 1959, prior to the initiation of cambial activity. This instrument was in operation through most of the 1959 growing season, and since its results have been highly satisfactory and several advantages over other growth measuring devices are now evident, it is briefly described. Its basic component is a Pancake Rectipot Potentiometer manufactured by G. M. Giannini. Co., Inc., Pasadena, California. This Rectipot (see Table I for specifications) is mounted within a small plastic housing and secured to the tree by adjustable screws anchored in the xylem. Since only two mounting screws are required, the electric dendrograph can be easily mounted on stems as small as 3 in. in diameter. The movable shaft of the Rectipot is held to the stem by a small screw in the outer bark; consequently any change in the outer radius of the tree causes an equal displacement of the shaft. Shaft displacement can be remotely measured as a change in electrical resistance which, in the Neotoma studies, is measured by a Leeds and Northrup multipoint strip chart recording ohmmeter. Table II contains data for 2 days collected from a red

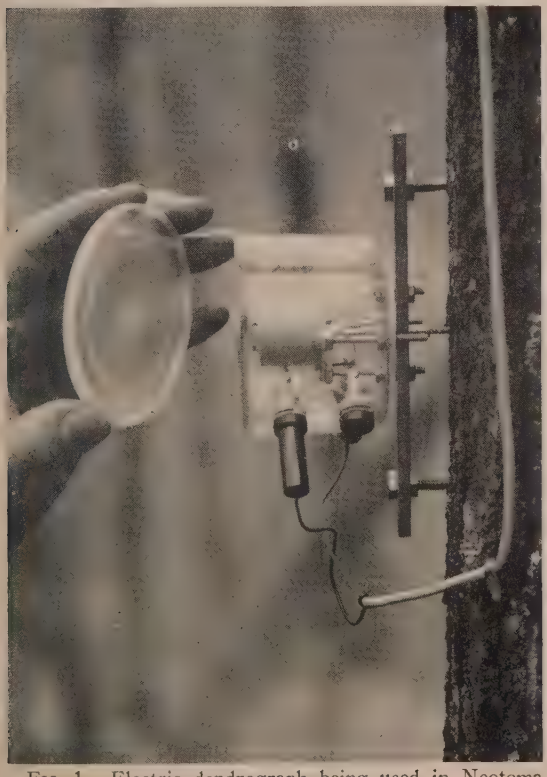

Fig. 1. Electric dendrograph being used in Neotoma researches concerning radial growth of woody stems.

Table I. Specifications of Giannini Model 86125 A-0.5-20 Pancake Rectipot Potentiometer.

| Resistance Range (ohms) | Body Size (in.) | | Stroke Length (in.) | Linearity % | Resolution (in.) | Temperature Coefficient |
|---|---|---|---|---|---|---|
| | Length | Diameter | | | | |
| 0-2000 | 0.94 | 0.97 | 0.500 | ±1 | 0.0011 | 0.00060 ohm/°C |

Table II. Bi-hourly radial change in thousandths of an inch of red oak stem as measured by electric dendrograph.

| Date | Hour | Change | Date | Hour | Change |
|---|---|---|---|---|---|
| 7/15/59 | 0000 | 0 | 7/16/59 | 0200 | 0 |
| | 0200 | 0 | | 0400 | 0 |
| | 0400 | 0 | | 0600 | 0 |
| | 0600 | 0 | | 0800 | −1 |
| | 0800 | 0 | | 1000 | 0 |
| | 1000 | 0 | (noon) | 1200 | −2 |
| (noon) | 1200 | −1 | | 1400 | 0 |
| | 1400 | −1 | | 1600 | 0 |
| | 1600 | 0 | | 1800 | 0 |
| | 1800 | 0 | | 2000 | +2 |
| | 2000 | +1 | | 2200 | 0 |
| | 2200 | +1 | | 2400 | +1 |
| | 2400 | +1 | 7/17/59 | 0200 | 0 |

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[2] A bioclimatic and ecological laboratory located in south-central Ohio.

oak (*Quercus rubra* L.) stem on a bi-hourly basis with readings to the nearest .001 in.

Advantages of the electric dendrograph over the various mechanical instruments being widely used include: 1) remote measurement reading or recording of radial change at one location of a great number of stems or stem locations; 2) any one of a variety of portable and non-portable measurement reading devices can be used; 3) small size: the dendrographs can be placed on stems of small diameter and/or in relatively inaccessible places such as high in a tree; 4) low initial cost of sensing element and housing (approx. $70.00); 5) ease and low cost of installation; and 6) maintenance involving only adjustment of mounting screws before each growing season.

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## VOLCANIC ASH CONTENT OF THE SOIL OF A *FESTUCA VIRIDULA* "BALD" ON A MOUNTAIN IN NORTHERN IDAHO[1]

### Introduction

Treeless mountain areas within otherwise forested regions are often referred to as mountain parks, or "balds." Balds are of common occurrence in northern Idaho, being encountered in the *Picea engelmanni-Abies lasiocarpa* (spruce-fir) zone, the highest belt of forests in the region (Daubenmire 1952). They usually interrupt the spruce-fir/Xerophyllum (SF/X) habitat type on south-facing slopes. The SF/X association is characterized by an understory of *Xerophyllum tenax*, usually accompanied by a considerable amount of *Vaccinium membranaceum*. The spruce-fir/Menziesia (SF/M) association occurs at corresponding elevations, but occupies the more moist north-facing slopes and limited areas of level and undulating topography. Subordinate vegetation consists predominantly of deciduous shrubs, usually dominated by *Menziesia ferruginea*.

Bald vegetation is generally quite distinct from that of the surrounding forest. Although a few scattered conifers may be present, in general they are old, stunted, and barely reproducing themselves. *Festuca viridula* is often very abundant, along with *Agropyron spicatum, Festuca idahoensis,* and *Hieracium albertinum. Prunus emarginata* may form a belt along the lower edge of the bald, where it comes into contact with the SF/X association.

The origins and maintenance of balds in the spruce-fir zone of northern Idaho have never been investigated. It is possible that they are relics of a vegetation previously more abundant on south-facing slopes during the postglacial xerothermic period. It has been suggested that their continued maintenance may be due to excessive dryness created by strong local winds, making the habitat too xeric for typical spruce-fir zone forest. Since soils of the region are known to contain volcanic ash (Secor 1956), and this important soil constituent was not deposited uniformly by the wind, an analysis of the glass content of surface samples from a single bald was undertaken in an attempt to elucidate the possible influence of ash upon bald distribution.

### Methods

The sampling site is located on Gisborn Mountain, within the Kaniksu National Forest, Idaho. A single north-south transect was laid out, starting at the upper edge of the bald and extending down into the trees along the lower edge. This transect also passed through a tree "island" located within the bald proper. Samples were taken from the upper 6 inches of mineral soil along the transect at measured distances apart, generally at 50 or 100 feet intervals. The very fine sand fraction (0.10-0.05 mm) of each sample was used for volcanic ash analysis.

Organic matter was removed with $H_2O_2$. Iron oxides were reduced and discarded using the magnesium ribbon-nascent hydrogen method of Jeffries (1947), as well as the procedure of Aguilera and Jackson (1953). Samples were dried, sieved, and mounted on slides using the method of Marshall and Jeffries (1946). Volcanic glass counts were made through the use of a petrographic microscope. At least 250 grains were counted for each sample.

### Results and Conclusions

Counts of volcanic ash in surface samples indicate there is a progressive decrease in this material with increasing distance down from the ridge top, lowest values being evident in the bottom part of the grassland and contiguous forest (Fig. 1). Counts are high near the upper edge of the bald, and compare favorably with those obtained from two surface samples located in the spruce-fir/Menziesia (SF/M) stand on the opposing slope (Fig. 1). It would appear that, similar to soils of the basal plain (Rieger and Smith 1955), high mountain ridges are characterized by unequal distribution of volcanic ash, with the thinnest deposits occurring on wind-ward slopes. However, location of grassland appears to be unrelated

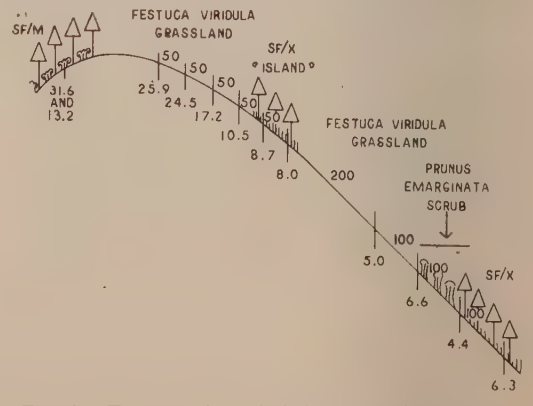


Fig. 1. Transect through bald on south-facing slope of Gisborn Mountain, Kaniksu National Forest, Idaho. Distances in ft between contiguous sampling points shown just above soil line. Per cent ash composition shown below sampling points.

[1] The author wishes to acknowledge the helpful suggestions of Dr. R. Daubenmire.

to content of ash in the soil, since the range of values (5-26%) is similar to that found for adjacent forest (4-32%).


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## AN EVALUATION OF TIMOTHY FLINT'S OBSERVATIONS ON THE OHIO AND MISSISSIPPI VALLEYS

Ecologists frequently need to reconstruct the original vegetation of the land that they are working on. Surveyors' records have become the chief tool for such reconstructions, but other historical records such as the observations of early travelers serve as a useful supplement and are particularly necessary for regions which were settled before any systematic survey was made. Unfortunately, however, the early travelers were rarely botanists and some of them were not even very close observers.

Rusk's *Literature of the Middle Western Frontier* (Rusk 1925) contains an invaluable bibliography of travel books and emigrants' guides which describe the Middle West, but most of them are both obscure and rare. Files of magazines published in the early part of the nineteenth century, *Knickerbocker's Magazine,* the *American Quarterly Review,* and *Graham's Monthly Magazine,* contain a good many descriptions of Western travel; and the magazines of the Middle West, the *Western Review and Miscellaneous Magazine;* the *Western Monthly Magazine; Western Monthly Review,* published by Timothy Flint, and the *Illinois Monthly Magazine,* published by Judge James Hall, were careful to review books of local interest in addition to publishing articles on the Western country. But the fact remains that the taste of the time dictated grandiose descriptions infused with conventional emotions and couched in the terms of painting rather than of botany. For example, James Paulding's article "The Illinois and the Prairies" (Paulding 1849) although less lush of prose than many such articles, contains an account of a journey up the Illinois River and then overland from Ottawa to Chicago across the richest prairie land of the Middle West; but Paulding admires some cows in a pasture outside Ottawa, exclaims over the beauty of the prairie lands while remarking that Bryant has sufficiently described them, goes on to recount where he lodged, and gets to Joliet and Chicago with all literary dispatch. After such an experience it is a relief to turn to the work of Timothy Flint.

Timothy Flint was a well-educated New England minister of liberal persuasion who went West in 1815 in search of health and a congenial parish. He never found either, but during the search he lived and traveled for more than twenty years along the Ohio and Mississippi Valleys. He journeyed most frequently by boat, but he sometimes went overland to preach an engagement; he settled for a time at Jackson, Missouri, at New Madrid, and the Post of the Arkansas; and on all his travels his interest in the land was so strong that he often quit the boat and went afoot, or on horseback, in the interest of close observation. After his period of active travel, he settled at Cincinnati for some years as a publisher and finally came to comparative rest on a plantation at Alexandria, Louisiana. The result of this peripatetic life was a series of highly romantic novels and three works of non-fiction: *The Recollections of the Last Ten Years on the Mississippi* (Flint 1826), and two editions of a geography which was so altered for the second edition as to comprise two separate works, *The Condensed History and Geography of the Western States* (Flint 1828) and the *History and Geography of the Mississippi Valley* (Flint 1832). The *Recollections* is wholly made up of his own observations and the *History and Geography of the Mississippi Valley,* he says, is more than half compiled from his own observation as a result of his effort to satisfy his readers by reducing the amount of history and enlarging the geographic description as an aid to emigrants (Flint 1832).

It becomes evident, then, that the value of these works to ecologists and plant geographers lies almost entriely in Flint's qualifications as an observer, and Flint was an excellent observer even by modern standards.

In the first place, he was familiar with the work of the naturalists of his time. He quotes Bartram and Nuttall, and refers his readers to "Bartram, Bradbury, Pursh, Michaux, and Nuttal [sic]" (Flint 1832). He mentions picking flowers and leaves for examination and in an article by him in the *Knickerbocker Magazine* (Flint 1835) there is a hint that he kept an orderly herbarium, for in an encounter with two obnoxious children on a voyage to New York, he speaks of having "my laboriously collected herbarium scattered leaf by leaf into the sea." This herbarium has never come to light, but if it escaped the ravages of these urchins and the destruction of Flint's papers in Alexandria during the Civil War, it may yet be discovered, possibly among the unfiled collections in some college storeroom.

In the second place, Flint saw plants not only as

isolated specimens, but as members of communities. In the *Geography and History of the Mississippi Valley* he differentiated between wet, dry, and bushy prairies, upland and alluvial woods, and barrens, and included sufficiently detailed descriptions to serve as proof that he did not use such terms loosely. It is interesting to note that Flint separates the prairies into "three divisions—the healthy, or bushy, the alluvial, or wet, and the dry prairies" (Flint 1832).

The reference to a bushy prairie occurs several times in his works, sometimes as a "hazel prairie," and he has included a slightly more detailed description of one such prairie at Florissant, Missouri.

> At Florissant there is a delightful small prairie, which has the appearance of having been in former days the bed of a lake. The soil is of extreme fertility and black as ink. Here are large tracts covered with hazel bushes, prairie plumbs [sic] and crab apple trees. The beauty and fertility of this place is indicated by the French name. (Flint 1826)

Since mention of the bushy prairies occurs most frequently in the northern, more populous, regions he describes, they may represent small prairies which in the course of succession were becoming forested. The further division of wet and dry prairies is one with which all ecologists are familiar and the aspect of the prairies, as he describes them, is equally familiar, almost reminiscent of Weaver.

> Most of the prairie flowers have tall and arrowy stems and spiked or tassellated heads, and the flowers have great size, gaudiness and splendor; without much fragrance or delicacy. The most striking of these flowers we shall atempt to class and describe, in another place; only remarking here, that during the summer the prairies present distinct successions of dominant hues, as the season advances. The prevalent color of the prairie flowers in spring is blueish purple; in midsummer red, with a considerable proportion of yellow. In autumn the flowers are very large, many of them of the helianthus form, and the prairie receives from them such a splendid coloring of yellow, as almost to present to the imagination an immense gilding. (Flint 1832)

Presented even in the general terms of the foregoing passage, this is a description of prairie, not of marsh. Therefore, when Flint writes in the *Recollections* that in Louisiana "next in order to the pine woods are the prairies of which there is a vast extent, scattered all over the region west of the Mississippi," one is forced to consider that it may have been so. He goes on then to a more specific location of these prairies.

> The parishes of Attakapas and Opelouses are principally prairie regions. The former has many sugar and cotton plantations, but is principally devoted to rasing cattle. The prairies differ little in appearance and character from those in the upper country. (Flint 1826)

Flint also uses the term "barrens" strictly, and in the *Geography* of 1832 provides a general description of this type vegetation.

> The country denominated "barrens" has a very distinct and peculiar configuration. It is generally a country with a surface, undulating with gentle hills, of a peculiar form. They are long and uniform ridges. The soil is for the most part of clayey texture, of a reddish or grayish color and is covered with a tall coarse grass . . . . the trees are generally very sparse, seldom large, or very small. They are chiefly of the different kinds of oaks; and the barren trees have an appearance and configuration appropriate to the soil they inhabit. The land never exceeds second rate in quality and is more generally third rate. (Flint 1832)

As would be expected, Flint often wrote descriptions of forest, and in many of these he is careful to list the trees of the area and also to remark on the similarities to, or differences from, adjoining areas. Thus, in descending the Ohio, he writes that at Steubenville the river,

> . . . . seemed to develop its character for broadness and fertility. Here we first began to notice the pawpaw, the persimmon and other new and beautiful shrubs and plants, peculiar to this climate. (Flint 1826)

He says of the upper courses of the Muskingum, Miami and Scioto,

> . . . . the forest trees are the same as in Kentucky and Indiana, except that the pecan tree, which is common on the waters of the Wabash, is not often found here. The forests are deep, but in the richest soils, the trees are rather distinguishable for their straightness than their size. (Flint 1832)

Of southern Ohio he writes,

> . . . . the prevalent kinds of trees are, the different species of oak, white, red and black; yellow and white poplar; all the different species of hickories; especially the black and white walnut; three species of elm, hackberry, buckeye, linn, and coffee tree. White maple is common and sugar maple of great beauty, almost universal. Beech, however, is the most common timber. The undergrowth is spice bush, dogwood, iron wood, horn beam, black haw, pawpaw, different species of thorn, and wild plum. (Flint 1832)

He almost uniformly indicates the 33° of latitude as the division between the southern forests and those about the Ohio.

> Below 33° commences the proper climate for cotton and it is the staple article of cultivation. Festoons of long moss hang from the trees, and darken the forests. The palmetto gives to the low alluvial grounds a grand and striking verdure. The muscadine grape, strongly designating climate, is first found here. Laurel trees become common in the forest, wheat is no longer seen, as an article of cultivation. The fig tree brings its fruit to full maturity. (Flint 1832)

> The chickasaw plumb [sic] is common from 34° to the Gulf of Mexico. It is found in the greatest abundance, and ripens early in June. Prairie plumbs are most abundant in Illinois and Missouri, on the hazle [sic] prairies, they are of various sizes and flavors. Their general color is reddish, and their flavor tart. Some of them are large and delicious. For an experiment of yield, two bushels were gathered from one tree. (Flint 1828)

The foregoing excerpts demonstrate that Flint's observations are sufficiently accurate and detailed to prove of use to ecologists, even though, as James Hall wrote approvingly, Flint uses the common names of trees and shrubs and does not write as a "professed naturalist" (Hall 1829).

The chief obstacle to using Flint's observations is the difficulty of locating the precise spot which he describes, a difficulty familiar to anyone who reads such early records. Some places were nameless when he wrote; some have had their names changed since that time, and some of the places he confidently used as reference points have vanished altogether. River names, however, were bestowed early and have remained relatively unchanged so that Flint's habit of locating sites

in relation to the nearest river makes it possible to identify many locations accurately.


### Summary

Timothy Flint's accounts of the Middle West from 1816 to 1845 are among the most extensive and accurate for ecological use of the accounts listed in the *Literature of the Middle Western Frontier* (Rusk 1925). Flint includes numerous accounts of prairies, including a type he refers to as "bushy," or "hazel," prairies; descriptions of forest types, of soils, and of species ranges. Consequently his work is a reliable source of description of the original vegetation of the Ohio and Mississippi valleys.


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## STANDING CROP OF HERBACEOUS VEGETATION IN SOUTHERN MICHIGAN

Few papers have been published giving data on the productivity or standing crop of herbaceous vegetation in the United States (Bray *et al.* 1959). During a study of the local distribution of small mammals in southern Michigan, data were obtained on the standing crop of herbaceous vegetation, primarily to determine the cover and food available in various habitats. Part of these data have been presented in connection with the mammal study (Getz 1959). Since such information is relatively rare in the literature, it seems advisable to make it available in greater detail.

I wish to thank Dr. W. S. Benninghoff for suggestions during the study and in the preparation of the manuscript. Dr. F. C. Evans also offered suggestions concerning the manuscript.

### Description of the Study Area

The standing crop was determined for several components of the herbaceous vegetation in 4 different habitats: a marsh, an abandoned field, a bog mat, and an upland hardwood forest stand. All were located in the University of Michigan's Mud Lake Research Area, Washtenaw County, Michigan.

*Marsh.*—The site of this stand is for the most part typical of marsh habitats. The surface is topographically low and poorly drained with the water table only a few centimeters below the surface. During the wet season (October through April) most of the area (included in the study) is inundated. The soil is typical of marshes (Dansereau 1957); it contains much fibrous, peaty humus and a moderate amount of mineral matter. The soil water content is high even when not inundated; it is nearly saturated during the driest months. The predominant sedges and grasses form small tussocks 5-10 cm in diameter. Each tussock is 5-10 cm tall.

*Old field.*—This is an abandoned field that has not been under cultivation for approximately 15 years. The last crop it produced was maize. There is a small depression with a drainage outlet in the northern part of the field. The outlet is bordered by a dense stand of sedges which was not sampled, as such vegetation is not typical of abandoned fields. The southern portion of the field slopes down to a point approximately 3 m below the field level. The soil is a sandy loam (Miami loam) except in the low, moist sites which have a slightly higher humus content. Sheet erosion on the slopes has removed most of the top soil, exposing sandy clay. The soil becomes very dry during the summer.

*Bog mat.*—The bog area is adjacent to the north margin of Mud Lake. It is a typical *Sphagnum* bog mat, soft and springy but able to support a man's weight. Several different plant communities occur, but the study was limited to an area in which the dominant plants (in addition to *Sphagnum*) were a sedge, *Carex lasiocarpa*, and a fern, *Dryopteris Thelypteris*. The water level is usually 10-15 cm below the surface except for small depressions in the mat where standing water is exposed. The subsurface material is, therefore, very wet at all times; it is composed almost entirely of decaying vegetation and is covered by *Sphagnum*.

*Upland hardwoods.*—This area is situated on an "island" lying in a low marsh. Its highest points are 4-5 m above the surrounding marsh. It is characterized by a mature oak-hickory stand with sedges and forbs predominant in the field stratum. The tree canopy is closed. Leaf litter and humus layers of the soil are well developed and there are numerous fallen trees in the area. The study is on a site where the field stratum is composed primarily of *Carex rosea*. Phytosociological lists of predominant plants of all 4 areas are given by Getz (*op. cit.*).

### Methods

Quadrats were located in each area so that representative samples of all variations of the vegetation in the study area would be obtained. When the approximate position for a quadrat was determined, a pair of clippers was thrown into the site. From the point where the clippers landed, the quadrat was aligned with sides parallel to the previously positioned quadrats. A square wooden frame with inside dimensions of one meter on each side was used to delimit the quadrat. Vegetation within the frame, regardless of where it was rooted, was clipped approximately 5 cm above the surface. Samples thus obtained were bagged, air dried, and separated for

weighing. Samples from all areas were processed at the same time.

Two series of samples were taken, one in March, 1958, the other in June (old field) and July, 1958 (marsh, bog mat, and upland hardwoods). All the summer plots were located adjacent to the March plots. Samples taken during the summer represent the peak growth for each area. Because of numerous standing dead stems of grass in the old field in June, it was not feasible to separate all living stems. To determine the standing crop for this area, the amount in the March samples was subtracted from the amount in the June clippings. These data were further checked by clipping 6 of the plots that were clipped in March. Although some vegetation may have decayed between March and June, comparisons with the yield from the plots clipped in March indicated it was not significant enough to bias the data.

The following number of plots were clipped in each series: marsh, 36; old field, 26; bog mat, 5; upland hardwoods, 5.

Water depths in the marsh were recorded at each plot in April, 1958. A greater portion of the marsh was inundated at this time than during any other month. The data obtained have been used to correlate the moisture present with the standing crop of vegetation. Although no standing water was present after July, 1958, the plots that had greater depths of standing water in April contained standing water later into the summer. Available moisture was, therefore, greater at these sites than at those on which the water depths were less in April.

## Results

The predominant species of sedges and rushes in the marsh were treated individually, and the standing crop of each was determined. The remainder of the sedges, the grasses (*Glyceria striata, Phalaris arundinacea, Calamagrostis canadensis*) and the forbs (primarily *Eupatorium purpurea, Impatiens capensis, Aster simplex,* and *Galium* sp.) were not separated according to species. The standing crop of each of the more abundant species in the old field (*Poa compressa, Potentilla intermedia,* and *Daucus carota*) was determined separately.

The standing crop for the marsh was 465 $\pm$121 gr/m$^2$ (Table I) as compared to 170 $\pm$36 gr/m$^2$ for the old field (Table II). This difference is significant at the .01 level (t.=3.88). The standing crop of forbs in the marsh was 75 $\pm$66 gr/m$^2$ as compared to 105 $\pm$30 gr/m$^2$ in the old field. This difference was not significant (t.=0.86). The standing crop of grasses in the marsh was 70 $\pm$93 gr/m$^2$ while that for the old field was 65 $\pm$58 gr/m$^2$. The difference was not significant (t.=0.24). The greater total standing crop of the marsh results from the several common species of sedges.

The standing crops for the bog mat and upland hardwoods are as follows:

| | | |
|---|---|---|
| | Bog mat | |
| *Dryopteris Thelypteris* | 115 $\pm$ 65 gr/m$^2$ | (40 — 175) |
| *Carex lasiocarpa* | 45 $\pm$ 22 gr/m$^2$ | (20 — 60) |
| | Upland hardwoods | |
| *Carex rosea* | 45 $\pm$ 8 gr/m$^2$ | (30 — 50) |
| Forbs | 5 $\pm$ 3 gr/m$^2$ | ( 5 — 10) |

The standing crop of sedges was, therefore, approximately the same on the bog mat and in the upland hardwoods. The standing crop of sedges in these two areas was significantly different (at the .01 level) from the total standing crop of sedges in the marsh (t.=2.84 and 2.73 for the upland hardwoods and bog mat respectively). The standing crop of *Dryopteris Thelypteris* in the marsh was significantly less (at the .01 level) than that on the bog mat (t.=4.72).

Table I. Standing crop of herbaceous vegetation and correlations with available moisture in a grass-sedge marsh.

| Plant | No. of plots in which it occurred | Standing Crop (gr/m$^2$) Mean | Range | Stand. Dev. | Correlation with moisture* | Probability** |
|---|---|---|---|---|---|---|
| *Carex lacustris* | 27 | 165 | 0-730 | 170 | +.44 | <.01 |
| *Carex* sp. (ovales section) | 6 | 40 | 0-310 | 89 | ..... | ..... |
| Misc. sedges | 5 | 20 | 0-240 | 48 | ..... | ..... |
| *Sparganium eurycarpum* | 11 | 45 | 0-430 | 104 | +.44 | <.01 |
| *Scirpus americana* | 4 | 10 | 0-200 | 40 | ..... | ..... |
| Grasses | 24 | 70 | 0-440 | 93 | −.20 | ..... |
| Forbs | 36 | 75 | 5-310 | 66 | −.53 | <.01 |
| *Dryopteris Thelypteris* | 22 | 30 | 0-105 | 38 | −.50 | <.01 |
| *Typha latifolia* | 6 | 10 | 0-220 | 32 | ..... | ..... |
| Total | 36 | 465 | 265-650 | 121 | ..... | ..... |

* Spearman Rank Correlation Coefficient.
** Level of significance.

Table II. Standing crop of herbaceous vegetation in an abandoned field.

| Species | Standing Crop (gr/m$^2$) Mean | Range | Standard Deviation |
|---|---|---|---|
| *Poa compressa* | 65 | 5-240 | 58 |
| *Potentilla intermedia* | 70 | 0-160 | 49 |
| *Daucus Carota* | 25 | 0- 90 | 27 |
| Other forbs | 10 | 0- 90 | 17 |
| Total | 170 | 110-260 | 36 |

Correlations of standing crop with available moisture are shown in column 5 of Table I. Correlations were determined by the Spearman Rank Correlation coefficient (Siegel 1956). There is a positive correlation between available moisture and the standing crop of *Carex lacustris* and *Sparganium eurycarpum* (significant at the .01 level) and a negative correlation (also significant at the .01 level) between the available moisture and the standing crop of forbs and *Dryopteris Thelypteris*. A slight, but not significant, negative correlation also existed between the standing crop of grasses and the amount of moisture present. Soil moisture data were obtained for the old field, but differences were not considered significant enough to attempt correlations with the standing crop.

## Summary

The standing crop of herbaceous vegetation was determined for four habitats in southern Michigan: a marsh, an abandoned field, a bog mat, and an upland hardwood forest.

The total standing of crop of the marsh was significantly greater than that of the abandoned field (465 and 170 gr/m$^2$). The standing crop of sedges in the marsh was significantly greater than on the bog mat or in the upland hardwoods (225, 45, and 45 gr/m$^2$ respectively). The standing crop of *Dryopteris thelypteris* was

significantly greater on the bog mat than in the marsh (115 and 30 gr/m² respectively).

In the marsh there was a positive correlation of the standing crop of sedges and rushes with available moisture. There was a negative correlation with the standing crop of ferns and forbs with available moisture.

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## EXPERIMENTAL GERMINATION OF SEED AND ESTABLISHMENT OF SEEDLINGS OF *PHRAGMITES COMMUNIS*[1]

Examination of the vegetation which volunteered on mud flats at the Mud Lake National Wildlife Refuge in Northwestern Minnesota during the summer of 1953 revealed seedlings of a grass which the senior author tentatively identified as *Phragmites communis* Trin. Identification was made on the basis of the seed coat adhering to the roots of the youngest seedlings. During subsequent conversations, the late Dr. Norman C. Fassett indicated that definite germination of this species had not been reported. This led the authors to attempt to germinate *Phragmites* seed in the laboratory and to label a number of the seedlings on the mud flats so they could be relocated and identified after they had matured.

Seeds used in the germination experiments were contained in seed heads collected from a group of *Phragmites* plants growing on one of the refuge dikes in September, 1953. Germination tests were conducted in the laboratory in St. Paul by selecting well-filled florets from the heads and placing them in petri dishes of tap water. Laboratory tests were made on samples of seed after 3-6 months storage. The 6 month's tests included seed which had been stored dry in paper bags at room temperature, seed stored wet in glass vials at room temperature, seed stored dry in glass vials at outside temperatures (alternate freezing and thawing during the winter) and seed stored wet in glass vials at outside temperature. No germination was obtained in any of these tests.

Additional tests were conducted after 7 months storage. Seeds were placed in corked glass vials that had been half-filled with water. These were set out of doors in a wooden rack at St. Paul, Minnesota, and exposed to normal variations of outside temperature and light in late April. Four such tests, which were conducted on seeds that had been stored wet at outside temperature, gave no germination. However, in 4 tests made on seed stored at room temperature for 7 months, seeds in 19 of 40 florets germinated, or an overall percentage of nearly 50 per cent. One further test was made on seed stored dry at room temperature after 8 months and 30 per cent of the seeds in 150 germinated.

Examination of the staked seedlings on the mud flats in late summer of 1954 revealed without any possible doubt that the plants in question definitely were *Phragmites communis* Trin.

While these germination tests were not of an extensive or large scale nature, they do show that *Phragmites communis* Trin. seeds can be germinated experimentally and document the establishment of seedlings in nature.

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## AN ORGANIZATIONAL HIERARCHY POSTULATE FOR THE INTERPRETATION OF SPECIES-INDIVIDUAL DISTRIBUTIONS, SPECIES ENTROPY, ECOSYSTEM EVOLUTION, AND THE MEANING OF A SPECIES-VARIETY INDEX

### Species-Individual Distributions

One of the most fascinating and heretofore unexplained properties of ecological systems is the widespread similarity in the numerical distribution patterns of individuals and species in communities. Not only are there a few species present with many individuals and many species present with a few individuals of each, but the common and rare are related in ways suggesting logarithmic functions. Some principal graphs used are the following:

*Number of species vs. number of individuals per species.*—Willis (1922) plotted species versus individuals per species, obtaining curves in a wide variety of communities which resembled hyperbolas superficially, but were shown by Fisher, Corbet, and Williams (1943) to more closely resemble logarithmic series.

*Cumulative species vs. logarithm of number of individuals.*—Gleason (1922) and Cain (1932) plotted species accumulated versus the area sampled to obtain the now

familiar species-area curve. With the species on a linear scale and the area on a logarithmic scale, many graphs are relatively straight (Vestal 1949, Goodall 1952). The counting of species per area was done to estimate the effectiveness of sampling for counting species.

Gleason (1922) and Williams (1944) also plotted species cumulated vs. the *individuals* found. Such graphs are independent of the size of the organisms, permitting the comparison of curves for the large and the small. For example, algae in Silver Springs (Yount 1956) may be compared with the trees of a rain forest. Fisher, Corbet, and Williams (1943), in an effort to obtain an accurate descriptive formula, compared such curves with the straight line that one obtains from a logarithmic series plotted on these same coordinates. However, Preston (1948) and Williams in a later paper in 1953 indicated criticisms of the logarithmic series as a mathematical description. For purposes of this paper this type of graph, of which Figures 1-3 show examples, is of greatest significance.

*Number of species of particular abundance vs. logarithm of abundance.*—Preston (1948) followed by Williams (1953) and Patrick, Hohn, and Wallace (1954) found a fit of species-individual data in a graph of the number of species having a particular abundance versus the logarithm of that abundance. Hump shaped curves were obtained which were compared with theoretical log-normal curves on the same graph.

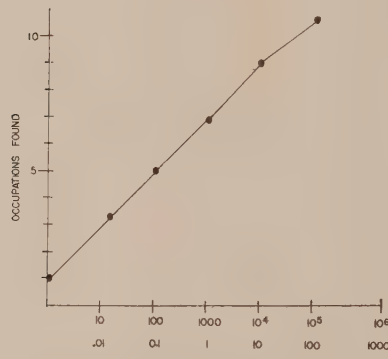


FIG. 1. Graph of occupations found versus logarithm of cumulative individuals counted based on the synthetic data which were formulated in Table I according to the hierarchy postulate of per capita relationship of occupations.

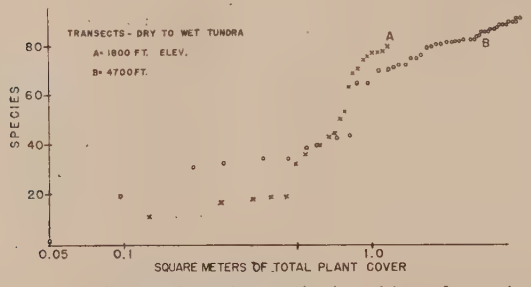


FIG. 2. Graph of species versus logarithm of cumulative cover of plants taken across conspicious environmental gradients in Arctic tundra. Cover rather than number of individuals is used where plant individuals are difficult to determine. Curve A shows two conspicuous rises as cover is accumulated from a dry hill top, down a moderate to poorly drained slope into a marsh. In curve B the middle type is poorly represented. These data are from a study aided by a contract between ONR, Department of the Navy, and the Arctic Institute of North America. Their reproduction in whole or in part is permitted for any purpose of the United States Government.

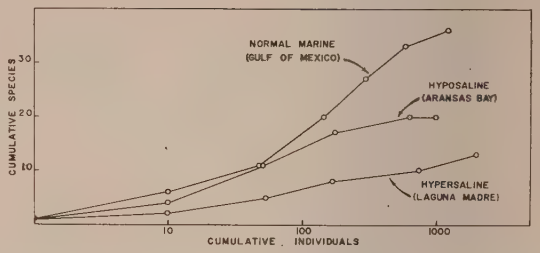


FIG. 3. Graph of species versus logarithm of cumulative individuals for molluscan shells in three marine environments of different environmental severity. Aransas Bay has low salinities; Laguna Madre has high salinities and the Gulf of Mexico has relatively normal and stable salinities.

*Abundance vs. logarithm of the rank.*—MacArthur (1957) and Hutchinson and MacArthur (1959) provided still another type of plot relating a measure of the abundance of a species to the rank order of abundance indicated on a logarithmic scale. The observed graphs were compared with some theotrical curves based on the hypothesis of a normal distribution of niche size. Difficulties with this and other plots are discussed by Hairston (1959). In all four of the types of graphs listed, logarithmic functions are involved.

## Species-Diversity Index

The logarithmic species-diversity index probably originated with Gleason (1922) and has been used by a number of authors (Fisher, Corbet, and Williams 1943, Williams 1950, Yount 1956, Odum and Hoskin 1957, Margalef 1957). It is the slope of the graph of cumulative species versus logarithm of individuals.

$$\frac{\text{Increment in cumulative species}}{\text{Increment in logarithm of individuals counted}} = \frac{\Delta S}{\Delta \log I} \qquad (1)$$

Fisher, Corbet, and Williams (1943) also considered the slope of the species-log individual graph as a proper measure of community species diversity particularly where the graph was straight. Since these authors postulated that the graphs were manifestations of the logarithmic series they used a constant derived from the logarithmic series for an index instead of the slope. One number may be derived from the other with the nomogram of Figure 8 of their paper. A table of standard error is also provided.

Even without theoretical implications, the slope of the species vs. log individuals graph is useful as an empirical measure of the diversity of communities. One may compare diversity of communities of all sizes, communities with different amounts of data, and communities sampled with different methods and sample sizes.

Recently Margalef (1957) has indicated that the logarithmic species diversity index (equation 1) has the mathematical form of negentropy (information). He

used the index to determine the amount of informational content in the plankton species of an estuary.

In the descriptive, graphical, and mathematical formulations so far presented to relate species and individuals there have been few efforts to indicate how the particular distributions come about and how such distributions are related to community function and survival (Goodall 1952). As Hutchinson (1953) stated, "It is likely that something very important is involved here, but for the present what it may be is a mystery." In later papers Hutchinson and MacArthur postulate that development of many species aids in establishing community stability. They attempt to show that the species divide the available spaces and niches in a random manner.

In this communication a different explanation is offered to account for the logarithmic properties of species-individual distributions cited above. The patterns are derived from postulates of a high degree of organization in nature, the very antithesis of random functions. However, Brian (1953) cautions ". . . lest the j-shape of the population form suggest to the ecologist intense interspecific competition, . . . it is well to recall that Kendal (1948) has shown that theoretically negative binomial distributions can develop where no competition or interference either between or within species occurs . . . [and] where immigration was . . . negligible the form tended toward that of a logarithmic series." Thus, it is perhaps prudent to assume that several kinds of phenomena may contribute to this logarithmic relationship including patterns which serve to regulate interaction.

## Functional Hierarchy of Occupations and Species

The proposed hypothesis can be presented as it was conceived using an analogy previously used by Elton (1926) in formulating a niche concept. The species in an association of organisms are compared to the occupations of humans in an army or in an urban community where something of the same distribution of commonness and rarity may occur. In such a community there is often a basic occupation that is the major reason for the existence of the community, such as agriculture or the making of some product in some central large industry. These workers and their occupations in the primary industry are most numerous. The occupations that serve and are dependent directly upon the basic occupation are less numerous such as wholesalers, truckers, salesmen, advertisers, and managers. Even further away functionally from the dominant occupation are those occupations that serve primarily the second stage occupations and are twice removed, such as special suppliers of specialized items needed in the secondary occupations. There may be even rarer occupations that serve only the third stage occupations and so forth. As one counts progressively more individuals one includes rarer occupations. The number of individuals who can make a living at the occupations far removed from the most common occupation becomes successively smaller. It takes an increasingly larger number of persons and an increasingly larger town to provide support for the more specialized jobs. This is natural since the cost of the most specialized services must be divided among those being served if the whole system is to have economic competitive value and not cause a collapse of functional chains due to inefficiency failure at some occupational link. Whether these comments about human occupations are exact or not, it is not the purpose of this communication to establish. The human analogy is used only in order to make the principle clear as advocated for ecological systems. Certainly the hypothesis applies to the table of organizations of military systems.

Many occupations such as grocers, druggists, and residential fuel suppliers service all of the others. The number of individuals in each occupation is not only due to the proximity of function to the basic occupations, but to the volume of occupational activity relative to the volume of basic function. Some occupations may be much more important to the community survival than their numbers indicate. Doctors, lawyers, teachers, and other specialists may be examples. In these cases as well as with the other occupations, the density of the occupation depends on the number of persons it serves.

Both in human communities and by analogy in biological communities, the occupational structure might be described as one in which the basic occupations which first bring energy into the system are determined by the energy and materials source whereas the remainder of the occupations are related on a per capita basis. Each dependent occupation has a definite and characteristic range in per capita requirement. There are ratios between each specialized occupation and the number of people being served.

## Hierarchy Postulate

As long as the rarer occupations are related to the commoner occupations in constant per cent ratios, the relationships of occupations to individuals is by definition logarithmic. The reason a plot of cumulative species and logarithm of cumulated individuals is a straight line in such a case is no mystery. If the per cent change in individuals with adding of species is constant, the following may be expressed.

$$\frac{dI}{IdS} = k \qquad (2)$$

Where $S$ is number of species and $I$ is the number of individuals. Integrating, the hierarchy postulate yields the following

$$\log I = kS + C \qquad (3)$$

and

$$S = K \log I \qquad (4)$$

which is a straight line on the plot of cumulative species and logarithm of individuals counted. The equation of the graph (4) is also the expression that Margalef recognized mathematically as of the same form as the expression for information where H is the information

$$H = K \log (\text{number of states}) \qquad (5)$$

(macroscopic negentrophy). Margalef (1957) comparing equations (4) and (5) reasoned that the number of species must be a measure of information. The reason that the number of species is a measure of the informational content now becomes apparent from the hierarchy postulate. Rothstein (1952) and others have shown that a hierarchy such as in a military organization could be described in units of information. An ecological heirarchy may be similarly described. Negentropy of information and organization of species are all measured by the same quantity. Constants in the equations are all different.

When a per capita hierarchy exists, organization exists, and equations 2-5 pertain. The degree to which these apply is the degree to which simple logarithmic, per capita structure exists. Since there is often some tendency for a straight line on graphs of species and log individuals, it must be concluded that to a considerable extent, communities tend to be organized into hierarchies in their relationships of species.

For an example consider the hypothetical table of

occupations in Table I constructed on the one single basic principle that each occupation requires a certain number of individuals to support it although the per capita requirement may vary greatly from one occupation to the next. Suppose that letters are used to represent occupations that are necessary to community survival. Three types of dependence are illustrated: occupational niches dependent on one other niche, occupational niches dependent on one other niche but requiring a large per capita support, and occupational niches dependent on the total number of all individuals present.

TABLE I. Some fictitious occupations and per-capita requirements for their support.

| Occupation | Number of other kinds of individuals required for support of one in this niche | Number of persons this occupational niche supported per area |
|---|---|---|
| A (primary occupation) | — | 1000 |
| B | 10 A | 100 |
| C | 10 B | 10 |
| D | 10 C | 1 |
| E | 10 D | 0.1 |
| F | 10 E | 0.01 |
| G | 10 F | 0.001 |
| H | 100 A | 10 |
| I | 100 B | 0.1 |
| J | 100 C | 0.001 |
| K | 100 D | 0.00001 |
| L | 10 A—n | 100 |
| M | 100 A—n | 10 |
| N | 1,000 A—n | 1 |
| O | 10,000 A—n | 0.1 |
| P | 100,000 A—n | 0.01 |

When the data in Table I are plotted as in Figure 1, a linear type curve results like those in many natural associations. The distribution of rarity in species tends to be logarithmic because directly or indirectly each rare species requires or is required by a definite number of the more common species for its survival and support. We might define a community as organized when the numbers of occupational niches are related on a per capita support basis.

Some of the successive hierarchy of relationship to the basic energy users may correspond to the trophic passage of energy. However, there are many routes of community coaction other than those involving major energy transfer, e.g., those concerned with transfers of materials or information. Such logarithmic hierarchy, thus, is not restricted to food chain relationships. It is likely, however, that any coaction involves an effect on energy budget.

The almost universal report of cases suggesting at least partial hierarchy of species indicates the universal similar organization of systems. Odum and Hoskin (1957) found organized cases in an artificial stream microcosm similar to those in nature.

## Deviations from Simple Hierarchial Organization

In many instances the graph of species cumulated versus individuals counted turns upward, turns downward, or has inflexions. There are several hypotheses which may be stated concerning the significance of such curves. A curve that turns upward has more organization and diversity than the straight (logarithmic) comparison line. A curve with downward curvature has less organization and diversity.

*Diversity with homogeneous sub-areas.*—An upward curve may be expected where one is counting in homogeneous small areas which are taxonomically different from adjacent homogeneous areas. As one counts, one is within the area of maximum functional interaction of species. With larger number of individuals counted one passes over wider areas and includes more than one homogeneous area thus including species at a faster rate than one would within a smaller area.

*Communities which are sub-organized.*—When the graph turns down (flattens) as the number of individuals counted increases, one may infer that there is less hierarchy than is possible. The system is under-organized. If organization has survival value for the system, such systems will have poor competitive value and be displaced by systems with higher organization. Under-organized systems may be expected where the environment is so new either in the invasion, successional, or evolutionary sense that adequate higher order species have not become established. The curvature and the slope of the curve in the upper zones is thus a measure of the degree of fulfillment and saturation of the evolution or growth of the organization.

*Inflexion and Edge.*—The graph of species and log of individuals or cover may be used to indicate discontinuity in organization of communities. Sharp upward turns of a graph indicate an edge (Figure 2).

The diversity of species may be related to the biomass counted or to the cover of the biomass as well as to the separate individuals. This makes it possible to count where the existence of separate individuals is uncertain as in Arctic ground cover (Figure 2). Such comparisons make possible comparison of the organization and the biomass.

## Species Diversity Index in Paleoecology

The considerations of diversity, organization, and the species diversity index may be used with fossil assemblages as well as with living systems. Since the species diversity index is independent of taxonomic content and little affected by dilution or concentration, it may be used to characterize the faunas of ancient seas. For example in Figure 3 shelled populations, living and dead from hyposaline and hypersaline environments with restricted diversity are compared with shells from a normal marine environment of the Gulf of Mexico. Such indices in ancient strata may help indicate the generality of logarithmic structure in past ages, the evolution of ecosystems with trends in organization, and the difference between normal environments and extreme ones.

## Summary

A postulate of per capita hierarchy of function in communities leads to logarithmic properties like those observed in many species-individual graphs. The hierarchy postulate explains why species-diversity index is a measure of organization in units of information and negative entropy as Margalef has postulated. The value of the organizational measure for paleoecology is illustrated with data on shells.

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# REVIEWS

## Fundamentals of Ecology[1]

There has been much discussion as to what ecology is, and what it ought to be. Odum defines it as the study of the structure and function of nature. It follows that ecology must aim at a synthesis, and that it sinks its roots into all other divisions of biology and science.

Practically all ecological research projects are bound to commence at the descriptive and analytical level; most also end there (degree conferred or difficulties cropping up) but a few are carried to their natural completion, i.e. to the point where the results can be interpreted in more general terms and gain importance for a much wider audience—mankind perhaps. Synthesis superimposed on sound premises means that another chunk of Nature has been *understood*, not just depicted.

The title of Odum's book is unique, and so are the contents. It is a textbook of ecology, but should perhaps rather be considered a catechism. Its distinguishing feature, as the present reviewer sees it, is that it guides the student towards a point of view; he is actively taught how to look at ecology and to search for the purring machine behind the detached facts. Structure and function of nature is the general idea permeating the book, and no student can possibly miss that point. This is achieved partly through a simple and straightforward language and partly through the fact that only a small number of (good) examples are used to illustrate the principles. The reader is never bogged down in examples, never allowed to forget what this particular example was meant to illustrate. With its emphasis on ideas and functional units it is a book of high pedagogical quality, a thought-provoking book likely to take the serious student right through the analytical and descriptive stage and far into the stage of synthesis and ecological understanding. Another merit is the quantitative element which enters into several of the examples and which is in harmony with trends in modern biology. H. T. Odum's share in this modern, quantitative outlook of the book should not be left unmentioned; the third chapter—on principles and concepts pertaining to energy in ecological systems—brings out very clearly that ecology offers exciting problems of fundamental importance for mankind.

The second edition follows the first in general layout: three parts (Basic ecological principles and concepts; The habitat approach; Applied ecology) subdivided in chapters built up on the model: statement, explanation, and examples. The coverage is remarkably good, all habitats seem to receive a fair share of attention, and so do the two general aspects of ecology: demography and production.

A good deal of new information has been included in the explanations and examples, this accounts for part of the growth that has taken place between the two editions. The chapter on terrestrial ecology has grown considerably, and it is no more a stepdaughter.

A chapter on radiation ecology is entirely new and adds a special feature to the book. "In the not too distant future, the radioecologist may well be one of those who must help decide when to contain and when to disperse the waste materials of the atomic age. If the ecologist does not know what to expect in the biological environment, who will?" These are the concluding sentences of the chapter on radiation ecology. During ages to come problems of radioactivity will enter into all scientific, economic, and political discussion, and human welfare may be at stake if mistakes are made. It is Odum's merit to have made these problems part of a general introduction to ecology. One may hope that ecologists may become more conscious of this aspect of ecology and also get engaged in carefully planned work along these lines. This hope raises the question if university training will undergo the necessary modification and turn out the desired type of ecologist. Ecology as we know it today is facing highly complex problems of transfer, metabolism and turnover of energy and matter through devious paths. This will also be true of tomorrow's radiation ecology, but in addition a high degree of responsibility will be associated with the discipline. One cannot wish for mankind to depend on ecologists for major decisions unless physics, chemistry, mathematics, biochemistry, physiology, etc. have played a more prominent role in their university training than is the case today.

The intelligent student who uses Fundamentals of Ecology is bound to feel that he needs a good training in the exact sciences; if he gets this training, ecology will offer fine hunting grounds; if he doesn't, Odum may find it difficult to prepare the third edition.

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[1] Odum, Eugene P. in collaboration with Howard T. Odum. 1959. Fundamentals of ecology. 2nd edn. W. B. Saunders Co., Philadelphia and London. xvii+546 pp. 160 figs., 32 tables. $7.50.

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## A Symposium on Human Ecology[1]

The massive volume which has resulted from the Wenner-Gren Foundation's impressive International Symposium on Man's Role in Changing the Face of the Earth is unusual among books of this sort not only because of its size and breadth but because of the amazing fact that it neither offers page upon page of urgent recommendations nor makes repeated eleventh-hour pleas for conscientious action. Readers looking at the book from a conservationist's point of view may be disappointed, in fact, that the 60 authors are able to discuss their subject in such a consistently unemotional fashion. This however, was the exact object of the conference, namely to bring together as many recognized authorities on man's tenure of the earth as possible in order to describe and

[1] Thomas, William L., Jr. (editor). 1956. Man's role in changing the face of the earth. (symposium) Published for the Wenner-Gren Foundation for Anthropological Research and the National Science Foundation by the University of Chicago Press, Chicago. xxxviii + 1193 pp., 180 figs. & 33 tables. $12.50.

calmly discuss the effects that man has had upon his environment. The hope was, then, that this exchange of ideas from all aspects of human ecology might bring new insight and broader understanding to a field which has suffered probably more than any other in science from the joint problem of lack of sound information and incessant demand for wise recommendation.

To judge from the contributed papers, which were not delivered at the meeting but were presented in written form and distributed to the entire select group well in advance of the actual conference, there was no dearth of interesting and challenging ideas. The breadth of their concern was truly remarkable. Insofar as attention was called to concepts and information which many of the participants may have had little opportunity to encounter before, the symposium must have been a tremendous success. The published record certainly accomplishes this for the reader.

The records of the discussions, which the planners had hoped would be the major contribution of the symposium, are rather disappointing, tending in many instances just to become abbreviated collections of subjective impressions, personal opinions, and homely anecdotes. It is impossible to discern whether this is the inevitable result of the condensation which must accompany summarization of discussion or whether the conference simply suffered from the "too-many-experts" syndrome, or whether (as the reader might be lead to suspect) the consistently important and therefore prodigiously busy participants simply had no time to read the background papers. One is left with the impression, however, that the discussions should have yielded much more than they did, that perhaps this group of proven experts might do well to try again now that there has been time to digest more of the amazing mass of information that was presented by and to them.

Topics were very intelligently selected and assigned by the co-chairmen (Carl O. Sauer, Marston Bates, and Lewis Mumford). Although some subjects appear to have missed the participants' real specialties, the symposium seems not to have suffered and may, in fact, have gained some stimulus for integration thereby. Man's involvement with grassland ecology, with fire, with accelerated erosion, and with climate seem to have received especially stimulating attention. The only consistent weakness noted by this reviewer was that many authors neglected the general theme in treating their specific topics. This seemed especially true of the anthropologists, many of whom continue to regard man as "mankind" (always enunciated with a deeply reverent tone) rather than an organism with normal environmental relations.

Special compliments are due to Mr. Thomas for his excellent job of editing. He and the others on the staff of the Wenner-Gren Foundation can take real pride in having created, in MAN'S ROLE, a work that will serve an active and entirely useful function in both the ecological and anthropological literature for many years.

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## PLANT SOCIOLOGY IN CENTRAL EUROPE

Knapp, Rüdiger. 1958. Einführung in die Pflanzensoziologie. Heft I. Arbeitsmethoden der Pflanzensoziologie und Eigenschaften der Pflanzengesellschaften. 2nd edn. Eugen Ulmer, Stuttgart. 112 pp., 34 figs., 17 tables. Paper DM 6.30, $1.50.

This thoroughly revised second edition on the properties and methods of plant sociology is divided into 6 sections: analysis of plant stands, construction and interpretation of sociological (association) tables, systematics of plant communities on the basis of species composition, synecology, succession and history of vegetation (synchronology), and geographic distribution. The clear, concise treatment, with numerous examples and 303 cited references, presents an excellent survey of principles and procedures widely used in Central Europe in analyzing and describing vegetation.

In the analysis of stands and the tabulation of data the Braun-Blanquet precedures are followed. Brief descriptions of each characteristic and method of measurement are given. In the classification of stands the use of various characteristics depends upon the problem and the viewpoint of the investigator. In Central Europe today the chief criterion is basically the species composition, particularly the degree of limitation of certain species to definite communities. In the identification of plant communities the chief criteria are the dominant species, differentiating species, and character species. The last group comprises the species in the 3 highest fidelity classes, as revealed by the sociological tables. Differentiating species are those that by their absence or presence can be used to separate communities that are otherwise similar.

The *association,* in the Braun-Blanquet sense, is the basic community-type into which stands are classified. The concept of this association has been narrowed in in recent years. Former geographical variations and subassociations have been raised to the rank of association. At present differential species and local character species play a more important role than formerly in identification. The higher categories, alliance, order, and class, have also been given narrower meanings.

Differentiating species are very suitable for indicating the smallest communities in different habitats and they are indispensable in systematic classification. The number of communities so identified, however, is very large. They are, therefore, less suitable for describing the vegetation of large territories because of the difficulty of gaining an over-all viewpoint. In order to meet this difficulty, while still retaining the Braun-Blanquet association and sub-units, Knapp proposes the *Hauptassoziation* (Principal-Association) and subunits. An example is the *Querceto-Carpinentum* (oak-hornbeam) Hauptassoziation occurring from western to east-central Europe, characterized by character species of high constancy such as *Carpinus betulus, Prunus avium,* and *Potentilla sterilis.* The Hauptassoziation is composed of *Gebiets-Assoziationen* (District-Associations) on the basis of differentiating species. Differences in species composition of the Gebiets-Assoziationen are determined chiefly by climatic conditions and floral history. Examples of Gebiets-Assoziationen in the *Querceto-Carpinetum* Hauptassoziation are the *Caricetoremotae-Fraxinetum alemannicum* (streamside ash-alder forest of the southern upper Rhine region) and the *Querceto-Carpinetum unstrutosaalense*

(oak-hornbeam forest of Central Germany). Minor subdivisions, characterized by differentiating species, are subassociations, variants, and subvariants. The facies is distinguished by dominant species. These minor communities are related to variations in edaphic conditions and stages in succession. Knapp emphasizes that these units can be differentiated only by extensive, comparative investigations of communities in the largest possible number of parts of a floral region. It has been possible to make this kind of a classification in Central Europe because of the abundance of analyses and sociological tables and detailed descriptions of associations in many kinds of vegetation. It cannot be used in North America at the present time because of the lack of the kinds of precise data that are required.

A geographic area containing certain "Haupt" and "Gebiets" associations and conditioned by certain climatic and soil properties is, according to Knapp, a *Wuchs-Gebiet* (Growth-District). For example, in the country between the Elbe and Neckar rivers, varying greatly in topography, there are 9 Growth-Districts, such as the spruce-district of the Thüringer Forest, the beech-district of the mid Rhine mountains, and the dry-district of the northern Rhine plain. In the first only the spruce "Gebiet" is found; in the second are 3 "Gebiets" with beech, ash, and alder prominent; and in the last are 5 "Gebiets" with oak, elm, and hornbeam. A certain Gebiets-Assoziation may occur in several Growth-Districts, and the latter usually contains several Gebiets-Assoziationen. Certain Gebiets-Assoziationen are regularly found adjacent to one another in the same district or topographic unit, but usually in different habitats. Such groups are designated *Wuchs-Zonen* (Growth-Zones) by Knapp. They are distinguished by the presence of "Haupt" associations which are present in one kind of "Wuchs" zone and absent in adjoining zones. They resemble the "formations" of F. E. Clements. The chief Wuchs-Zonen of Europe (excluding the extreme southern, southeastern, and western parts) are the evergreen sclerophyllous woody vegetation near the Mediterranean, the *Quercus pubescens* "zone" in southern Europe from Spain to the Balkans, the *Quercus-Carpinus* mixed forest from England to east-central Europe, north to southern Scandinavia and southeast to the Balkan Pennisula, the mountain-*Fagus* forest in the mountains from northeastern Spain to the Carpathian and Balkan mountains, the *Picea* forest at higher elevations in the mountains in central and southeastern Europe and most widespread in Fennoscandinavia and northeastern Europe, the *Empetrum* "zone" containing open woods and dwarf shrubs at high elevations and similar in distribution to the preceding, and the arctic-alpine "zone" above tree-line in the mountains and north of tree-line in northern Europe.

We are indebted to Knapp for this clear exposition of present-day plant sociology in Central Europe. The book gives one an excellent idea of the high state of development of vegetation knowledge in Central Europe, and the use made of this knowledge in agriculture, forestry, and vegetation-mapping.

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## Norwegian Mountain Vegetation and Its Ecology[1]

The Rondane district is a mountain massif in southern Norway 230 km north and 70 km west of Oslo (at 62° N latitude and 10° E longitude) rising to 2183 m from surroundings of 700-900 m. The area studied is less than 20 km wide in any direction. Dahl's vegetation monograph is a splendid and intensive study of this small, floristically poor, and pedologically unproductive area. Monotony is not really a characteristic of this vegetation, for Dahl organizes 440 stand surveys into 66 different vegetation units in 8 orders, 15 alliances and 43 associations.

Dahl is known to many American ecologists from his visit here in 1953. He also spent a year in Great Britain. He contrasts Scandinavian viewpoints on vegetation and ecology with Anglo-American views, but his "Anglo-American ecology" may seem an echo from the past to many. Do Americans still base all their vegetation studies on plant succession? Do Americans doubt that classification of vegetation must accompany successional studies? Do Americans really doubt that vegetation classification—in continua, gradients, sequences, or functions as well as associations—is possible? If the answers to these questions are yes, they indicate a profound parochialism accompanying ignorance of abundant ecological and vegetation literature in which such questions have been thoroughly discussed.

[1] Eilif Dahl. 1957. Rondane: Mountain vegetation in south Norway and its relation to the environment. Skrifter Norske Videnskaps-Akademi i Oslo. I. Mat.-Naturv. Klasse 1956 (3):1-374. (H. Aschehoug & Co., Oslo). $8.00.

The Rondane monograph is an admirable combination of vegetation classification and ecologically directed observations and measurements. Each activity is shown to be necessary to the other. Dahl gives priority to vegetation classification because this "is also an ecological tool to facilitate recognition of the factors of importance to the vegetation" (p. 79). "The repeated occurrence in nature of vegetational discontinuities is, in the writer's opinion, the basis which makes a real classification of vegetation possible. If all vegational changes were gradual, each species reacting independently to the external factors, there would be no basis of classification, only of typification" (p. 27).

A comprehensive picture of vegetation variation also results from classification. When variation in vegetation is found, sampled by stand surveys, and these are organized by a system of classification into units documented by association tables, then the names given to the units make possible reference and generalizations. Meaningful generalizations of ecological relationships are hardly possible otherwise.

Dahl even finds vegetation classification valuable in purely statistical studies of distribution of plants, of pattern in vegetation. It has frequently been said, and truly, that statistical methods cannot be of value in defining the vegetation units of a classification. They can be used to test the differences between such units for significance. Statistics requires a defined population within which to operate; it does not offer the definition. However, classification of vegetation can aid statistical studies. For example, in studies of pattern it is neces-

sary not to confound ecological and biological kinds of pattern. That there is an ecological basis for pattern in vegetation is the fundamental assumption of ecology. Dahl says, with tongue in cheek ". . .it has been possible in Rondane to make stricter demands on environmental uniformity than is usually possible because ecological investigations were carried out at the same time as the statistical" (p. 32).

The most precise means of selecting ecologically uniform areas for investigation is through vegetation classification.

Finally, if differences in vegetation, which become evident to the investigator and can be made evident to others through vegetation description and classification, can be related to environmental factors, and these factors "can be influenced by the activity of the plants, then dynamic relationships will emerge as a result of the analysis, but the approach is not restricted to this. A broader basis of attack is required than the dynamic approach alone can provide" (pp. 23-24).

It is not often that a regional vegetation monograph can serve as an advanced text in plant ecology. Dahl's can. With his earlier paper with Emil Hadač (1949. Homogeneity of plant communities. Stud. Bot. Chechoslov. 10: 159-176) Dahl has given an excellent treatment of many statistical methods in vegetation and ecological research. In the Rondane monograph is a good discussion of distribution of individual plants, and little is left to say on species-area curves. A constant of this curve, the index of diversity, is related directly to distribution of frequencies. Homogeneity of vegetation stands is related to homotony of vegetation types. Thus the relative sizes of constancy classes is a function of the index of diversity of vegetation types. Finally, the index of diversity is related to Sørensen's index of floristic similarity. The index of diversity is thus a most useful vegetation parameter. This index is the slope of the line obtained when species number on the ordinate is plotted against the logarithm to base *e* of corresponding areas in $m^2$.

Dahl classifies the vegetation of Rondane to subassociations. For each unit is given the mean number of species per stand, the index of diversity, and an association table. The tables contain the conventional ecological information for each stand, covers by layers, numbers of species of vascular plants, bryophytes, and lichens in each stand, and the species lists. For each species in the association tables is given its constancy class and average of the scale values for cover, called dominance. The Domin scale of cover is used.

The stands are located geographically by the "Read right up" method of coordinates. That is, since the accompanying 1/100,000 topographic map lacks a geographical grid other than latitude and longitude, the locations of individual stands are given by the distances in mm from the left and lower margins of the map. It is fascinating to plot on the map the locations of stands of one vegetation type and watch the topographic limitations of this particular kind of vegetation come alive.

Sørensen indices for all possible combinations of 37 dry land and for 23 mire and spring vegetation types are tabulated. Four separate indices are calculated using species dominance, presence, constancy, and constancy greater than 40%. In general the Sørensen indices seem to bear out the relationships and circumscriptions of the vegetation units arrived at by floristic similarities. They show some additional cross-similarities that hierarchial linear classification cannot show. However Dahl includes numerous tables showing for *groups* of alliances or associations their characteristic, preferential, differential, and regionally characteristic species.

A discussion of each vegetation unit includes nomenclature, ecology, relationships, geographical distribution, soils, and references to previous descriptions. Ecology of the vegetation is discussed in 82 pages under the headings of snow cover, solifluction, drainage, soil factors such as kinds of parent rocks and pH preferences and ranges of variation of the species, hydrology of springs, ecology of mires, and succession.

The monograph concludes with a species list, giving notes on distribution and ecology. It is difficult to overemphasize the amount of autecological information contained here, in the discussions of the various kinds of vegetation, and in the association tables.

Dahl's monograph is a rich source of information both for the ecologist interested in general concepts and their documentation and for those interested in a systematic account of some boreal vegetation and its ecology.

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## The Forest Community[1]

In an era when the current "modern biology" is at the molecular level it is stimulating to read two good books at the community level. These two have little in common except they are both relatively small in size, deal with certain common aspects of sylvan ecology, and are competent.

Neal's little treatise is an idyl. Mr. Neal is head of the Science Department of Taunton School in England. He has written his book for advanced high school and college freshmen students (sixth form-first year university), but hopes that it will be useful to naturalists generally. It covers about four years study of Thurlbear Woods, part of the Crown Lands. This forest is roughly an H-shaped tract of some thirty-two acres, near Taunton, Somerset County. It is primarily an open canopy oak (*Quercus robur*) forest, with much hazel (*Corylus avellana*) in the shrub stratum. This is a study of the whole forest, in which higher and lower flora and fauna are examined from the viewpoint of a number of principles.

There is no sense of urgency here; no Wheelerian hierodules garbed in *directoire* robes awaiting the latest line on productivity; no deeply instructed group thrilling to a new terminology of a behavior cult. Instead one is

[1] Neal, Ernest. 1958. Woodland ecology. 2nd edn. Harvard University Press, Cambridge, Mass. xii + 117 pp., 16 figs., 8 plates, 7 tables. $1.75.

McCormick, Jack. 1959. The living forest. Harper & Brothers, New York. viii + 118 pp., figs. $3.95.
figs. $3.95.

barefooted, padding over the forest floor and enjoying the shade. The author is aware that in such a small book many aspects must be touched upon too briefly, some not discussed at all. It is a valuable lesson in calculated compression and the reviewer read with the same sort of stimulus he experienced many years ago in reading Charles Elton's first edition of his ANIMAL ECOLOGY.

After Thurlbear Woods is discussed briefly in general terms, the flora is described in considerable detail relative to the size of the volume. This chapter is notable in its derivation of certain ecologic correlations from the annual cycle of vegetational events. It covers frequency, photosynthetic period, life form, phenology, types of pollination, and the production and dispersal of seeds. This third chapter is followed by physical and biotic factors within the forest, including light, atmospheric humidity, temperature, wind, soil and faunal actions. The food web is discussed but there is little attention paid to the dynamic aspects of the flow of energy through the several trophic levels. This could be considered a shortcoming, but the author had stated previously that everything could not be covered and that some things would be emphasized at the expense of others.

The chief animal habitats of Thurlbear Woods are noted and there are at least four chapters devoted to adjustments (competition and feeding adaptations, protective adaptations, adaptations relating to reproduction and life history, and dispersal adaptations). This is followed by a short chapter on population numbers and, in the second edition, a chapter on plant succession. Also in this edition the bibliography was extended to include a number of local articles on the taxonomy of the biota. There are some 73 of these titles, all on British plants and animals since the author realizes that "One of the biggest problems of any ecological study is the identification of the flora and the fauna" (p. xii). This is a realization, the profundity of which unfortunately is not often enough understood.

The book closes with a few conclusions. One is that the whole woodland community is a three-dimensional puzzle the shape of which is determined by the floral scaffolding; that there is an essential fluidity in what at first appear to be rigid relationships; the pieces of this gigantic puzzle may be viewed at times as amoeboid, altering through adaptations to changing conditions within the community—at times as a consequence of rhythmic daily and seasonal changes. Second, that there is an interdependence between the many parts of the whole, with the concomitant shifts in biotic balance so well known to students. Finally, the superimposition on the above two patterns of the dynamic nature of the whole, "its potential power for expansion and its intricate links with other surrounding communities . . . so we are led to the conception that all life is really a unit—a magnificent complex of interrelated parts, the full beauty of which is beyond all powers of comprehension" (p. 104). Of practical value is a four page Appendix concerning suggestions for studying forests. There are a bibliography and an index.

The book by McCormick has a much larger page size and the type is larger and more easily read. It too is well written, but since it deals with many types of forest and with applied as well as basic aspects, it lacks the beautifully integrated punch of Neal. On the other hand, it may be of more value to a student at the operational level of forest study in general.

The volume was derived from the exhibits in the new Hall of North American Forests opened in May, 1958 in the American Museum of Natural History. The forest as a community is developed in three chapters; 1 (Nature's City), 2 (The Life of the Forest Floor), and 5 (Weather in the Forest). All of these are good, and the fifth chapter is admirable, containing information on daily variation in the stratification of temperature which is novel in presentation. Throughout the book material in the text is enhanced by a profusion of diagrams and photographs. Unfortunately, these are not numbered.

The reviewer must take exception to one statement: "And there is a distinct diurnal pattern of activity in the forest city—bustling by day, quiet at night" (p. 11). It has been the reviewer's conviction, after years of study of forests in temperate and tropical America, that forests are anything but quiet by night.

Chapters 3 (Forest Insects) and 4 (Forest Tree Diseases) deal with forest pathology. The forest types of North America are discussed briefly and cogently in Chapter 7. The last two chapters have to do with harvesting the forest, but from two different points of departure. Chapter 8 (How Nature Harvests the Forest) deals with periodic harvesting by influences other than man. For example, there is a slow harvesting which may take several years as brought about by attack of the Engelmann spruce bark beetle; or there may be rapid destruction of large areas by fire and wind, followed by natural reforestation. Chapter 9 (Man and the Forest) has to do with lumbering. It is full of data not often assembled concisely, and describes three methods by which timber is harvested, *e.g.*, the clear cutting method, the seed tree method, and the selection method. Good conservation practice is implied throughout. There is an index, but no bibliography.

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## EXPERIMENTAL PLANT ECOLOGY[1]

Although preoccupied with describing the spatial distribution of organisms, plant ecology has increasingly felt the need for deeper penetration into the nature of these distributions. Dynamic ecology concerned first and foremost with causes and processes has increasingly subjected field interpretation to laboratory analysis. Ecology extending into the realm of experimentation has borrowed the techniques of the physiologist, the geneticist, and the morphologist.

Among the newer approaches to physiological ecology, those of F. W. Went are exemplary. His efforts at The Earhart Plant Research Laboratory while at the California Institute of Technology have provided a unique research facility. The visiting investigators, an international group of physiologists, geneticists, morphologists, and ecologists, using the controlled habitats are listed

[1] Went, F. W. 1957. The experimental control of plant growth. Chronica Botanica Co. (Chronica Botanica vol. 17), Waltham, Mass. xvii + 343 pp., 71 figs., 25 plates, 21 tables. $8.50.

in Table 5, pages 70-73, along with their institutions, years spent at the Earhart Laboratory, and the subjects of their investigation. This scientific roster is a tribute to Dr. Went's contribution to plant ecology as well as to related fields.

Dr. Went treats his subject, The Earhart Plant Research Laboratory, broadly—its construction, its operation, and its research. The first of three parts, a must for those considering adding a growth chamber to their research facilities, deals with the construction and operation of the Laboratory. The costs given in the conclusion of the book are probably out-dated because the publication date is 1957. The second part deals with the climatic responses of a number of different kinds of plants, the majority being agricultural or horticultural types. Two contributions deal with native plants, William M. Hiesey's treatment of grasses and Henry Hellmers' treatment of chaparral plants. The third part is a general discussion of the problems of plant growth. It includes an evaluation of variability, both genotypic and phenotypic, an analysis of germination, photosynthesis, nutrition, water relations, smog, and periodicity. Also included in the third part is a chapter dealing with measurement of water loss by W. C. Ashby and a chapter on biochemistry by A. W. Galston. Chapter 17 is entitled "Plant Climatology," and Chapter 18 is "Ecology."

As an autecological exposition primarily concerned with the biological individual, this work stands in sharp contrast with current autecology textbooks which fail to clearly focus the organism midst the mass of meteorological, pedological, and other data. The isolation of the discussion of ecology in Chapter 18, however, indicates a certain lack of integration of ecology with the various other subjects. In the introductory paragraph of Chapter 18, for example, it is noted that the "relationship of the individual species, variety, or ecotype to its surroundings," the "autecology," has been described for a limited number of plants in Chapters 6-14. As indicated by this statement, much of the material in the second part is of an ecological nature. For discussion under the chapter on ecology, Dr. Went has selected the following: temperature, nyctotemperature, climatic basis for sharp boundaries in the distribution of plants, soil temperature, seasonal thermoperiodicity, germination controlling plant distribution, rain, photoperiod, photosynthesis. His examples are varied and valuable.

The obligate, aerobic ecologist may find that growing plants in nutrient cultures under artificial air-conditioning and without other plants and animals is somewhat out of his realm of interest. For those whose ecological bent allows interest in plants of all kinds, from *Aloe* to *Zea*, and whose ecological goal is a better understanding of the relationship of plants to their surroundings, experimental or otherwise, this work offers a wealth of information.

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## CONTRIBUTIONS TOWARDS THE AUTECOLOGY OF A PLANT FAMILY[1]

It is seldom that a single family attracts the attention of a group of experts, but in the case of the subject of this book, the orchids, the extraordinary horticultural interest which these plants have invoked over the past century and more justifies the effort. The book is a series of chapters, each written by different authors, under the able editorship of Carl L. Withner of Brooklyn College. No attempt was made to maintain a uniform style, but this did not produce any difficulties, except for a certain amount of duplication.

Each chapter is essentially a review of existing knowledge of the subject of the chapter. The uneven autecology which results from this method is thus largely a reflection of the absence of publications on the aspects which are missing. Most of the work on orchids has been done by horticulturists under horticultural conditions, and this work has been largely concentrated in the fields of genetics, seed germination, and disease control. There are four chapters dealing with genetics and cytology, two with seed germination, and three with disease and pest control. Taxonomy, morphology, and physiology each have a single chapter. The concluding chapter deals with vanilla, the orchid of commerce. While all the chapters maintain a rather high standard, two seem worthy of special mention. Helen Adams' abundantly illustrated account of variation in the orchid flower should be of great value to students of evolution. The chapter on cytology by Robert Duncan is a scholarly dual approach to the subject, written so that both amateur orchidologists and professional cytologists may benefit from it. There is a voluminous appendix containing a very useful translation of Schlechter's key to the orchids, a list of the known chromosome numbers of orchids, and a list of formulae for orchid culture media. As can be seen from this list of topics, there is nothing on the phytosociology or environmental requirements of orchids in their native habitat.

In spite of this serious omission, there is much that can be learned about the autecology of orchids from this treatise. Temperature and photoperiodic control of flowering, conditions necessary for germination, nutrient requirements of mature plants, methods of vegetative reproduction, pollination and seed production, and other similar information is presented in the various chapters. Practically all of this autecology was derived from studies of tropical orchids grown under conditions of no-competition in greenhouses in the temperate zone and should be applied to the plants in their native habitat only with great caution.

The editor did not intend to produce a book on the ecology of orchids, but only to summarize the available scientific information on this interesting family. Viewed in this light, it can readily be asserted that he has succeeded to a remarkable degree and has produced the best work on the subject since Schlechter's[2] complete treatment of the family.

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[1] Withner, Carl L. (editor). 1959. The Orchids: a scientific survey. (symposium) Ronald Press Co., New York. vi + 648 pp., 144 figs. $14.00.

[2] Schlechter, R. 1927. Die Orchideen. 2nd ed. Parey, Berlin.

## Range Management for the Animal Ecologist[1]

Range management is a discipline which is composite, relying simultaneously and strongly on several areas of basic research in biology; but in a sense this is one of its merits, since the specialized views of any one of these research areas cannot dominate without distorting perspective about soil-plant-animal relations. As a discipline which applies ecological principles to man's utilization of grassland resources, it is often dismissed by the "pure" ecologist as having little to contribute to theory. A glance at Jack R. Harlan's book[1] will quickly reveal how false this impression is. Although the book is designed primarily as a text for courses in Forage Crops and Range Management, our purpose is not to comment except briefly on its suitability for its intended role, but to draw attention to certain information gathered by range managers of extraordinary interest to animal ecologists working with herbivores such as insects, rodents, and ungulates which utilize nutritionally poor forage.

The first three chapters summarize certain principles of geography and ecology as they apply to grasslands. These chapters seem inadequate and narrow in approach. Thus, for chapter 1, no mention is made of factors other than climate in the distribution and histories of grasslands; reference to Sauer's and Malin's ideas would have balanced the approach and added to the appeal of the subject matter to the student. In chapter 2, not only is there excessive terminology, but methods of describing and analyzing vegetation other than those of the Clementsian school might have been mentioned. These chapters need to be expanded in several respects to put them on a par with other parts of the book and so to make the whole more appropriate for the advanced courses which the author had in mind.

There then follow chapters devoted to the taxonomy, evolution and distribution of grasses and legumes. Other chapters deal with principles of plant physiology, animal nutrition, properties of soils, and mensuration of forages. The last two chapters take up particulars of range and pasture management, respectively. This review is concerned mainly with the chapters devoted to plant physiology and animal nutrition.

For the animal ecologist, knowledge of the nutrient content of forages and places of storage of nutrients, along with other facts to be mentioned, is relevant to several current arguments regarding regulatory mechanisms in natural populations. Range managers tell us that grasses store food chiefly above ground in leaf sheaths, stem bases and stolons, while legumes store food chiefly underground in tap roots and rhizomes where it is less available to animals on the surface of the ground and so less vulnerable to depletion by overgrazing. Nutrient content varies with age, the content of indigestible lignin increasing steadily.

The different methods evolved by animals to use microflora as an aid in digestion of coarse forage are not all equally successful. For example, the rumen is much more efficient than the caecum. Cattle can digest up to 80 per cent of unlignified crude fiber while horses can hardly digest more than 35 per cent. Swine and birds such as chickens are even less successful than horses. This fact is significant to students of gallinaceous birds, and one would like to know how rodents compare with other mammals. Other variations in digestibility are related to protein content of food. For example, sheep can digest only 20-30 per cent of protein when the ration contains only 3-5 per cent protein whereas 70-80 per cent can be digested from rations containing 20-25 per cent protein. Thus, as quality of the food decreases, efficiency of utilization decreases, a fact which could well be responsible for some population crashes in the wild. Other factors, such as lowered digestibility with increased fiber content in maturing vegetation, can aggravate this.

As if this were not enough, digestibility is also influenced by the balance of the ration, the amount of food consumed, and other conditions. Furthermore, since digestion requires energy on the part of the animal, the net gain may be much less than the gross intake. For example, though wheat straw is about 40 per cent digestible, it requires so much energy to digest that very little energy is left for anabolic purposes.

Even nutritionally rich vegetation may be deficient in particular vital elements. Phosphorus deficiencies are widespread in grassland regions, and drought further reduces phosphorus availability. Also, since the optimum Ca/P ratio varies with the age of the animal, it could be responsible for some differential mortalities observed in the wild. Sodium deficiencies, almost always assumed to exist in pasture forage by ranchers, are known to reduce fertility and the ability of animals to use protein and carbohydrate foodstuffs. The effects of sodium deficiency on wild animals have apparently never been investigated. Chlorine is also almost universally deficient, but its effects are less well known. Cobalt deficiency, which is also widespread, has detrimental effects upon intestinal microflora.

The importance of these types of information, well known to range managers but often neglected by other ecologists concerned with factors governing animal numbers, cannot be overemphasized. Most species of animals displaying pronounced population cycles are herbivores using food similar to that utilized by range animals, and cycles are currently the subject of much research and debate. All too often, an analysis of the capacity of the environment to support the species in question is limited to a brief foray into the field at which time it is observed that the ground is well covered with vegetation. Having thus satisfied himself that food is not limiting, the investigator then proceeds to search for other causes of population limitation, such as predation or social interactions within the population. In the light of the good documentation on the complexity of utilization of grassland vegetation so handily packaged in Harlan's book, the present emphasis on hypotheses having to do with these other causes seems to us unjustified. Yet, for microtine rodents, there is more in the literature on adrenal size than on their nutrient requirements.

Any animal ecologist unacquainted with the field of range management should read Harlan's chapters on plant physiology and animal nutrition. Those concerned with control phenomena in natural populations can use them as entrées into an important literature. Clearly, without sound information on the nutrient status of vegetation and nutrient requirements of particular herbivores, it is not possible to interpret validly other findings concerning the physiology and behavior of their populations. Jack R. Harlan's book can and should play a vital role in a portion of ecology where it may have been least expected by the author.

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[1] Harlan, Jack R. 1956. Theory and dynamics of grassland agriculture. D. van Nostrand Co., Princeton. x + 281 pp., 26 figs., 7 plates. $6.75.

## The Brown Coal Formation of the Lower Rhine: Paleontological and Paleoecological Aspects[1]

Certainly few if any geographic areas of the earth, nor units of sedimentation and geologic time have received the exhaustive treatment encompassed by this work. Although the book is predominantly geologic in intent and flavour, there is a wealth of information regarding fossil flora and fauna which is of direct ecologic interest, in particular to students of paleoecology and biogeography. The reader is continually impressed with the extent to which paleontological data is utilized in unravelling the story of this complex sedimentary basin of the Lower Rhine, which contains the vast brown coal deposits (lignite in U. S. terminology) of West Germany.

The work is divided into two major parts of approximately equal length. Part I deals with Oligocene sediments of the North Sea in the northern part of the Lower Rhine basin. This part, essentially a book in itself, comprises 37 separate contributions, many of which deal with purely sedimentological and stratigraphic aspects of the basin complex. Included, however, are more than a dozen papers concerned with invertebrates and vertebrates, as well as microfossils of both plant and animal groups. Treatment ranges from such well known groups as the ostracods and foraminifera through much less well known, or less common fossil forms as coccolithophorids and the otoliths of fishes. For the most part these papers are copiously and excellently illustrated with both line drawings and half-tone plates.

The second part of the volume is mainly concerned with the continental or non-marine deposits of Oligocene and Miocene age in the southern part of the Lower Rhine basin. Here are to be found those aspects of the work which are of most interest to paleobotany, plant geography and ecology. The main theme around which the numerous contributions are built is that of the brown coal itself; its structure, composition, mode of origin, tectonics and its botanical source materials. The subject is treated in exhaustive detail. Since coal is formed almost exclusively of plant material there is a wealth of paleobotanical information presented, with respect to pollen grains, leaf cuticles, wood, fruits and seeds. In the aggregate an impressive list of generic entities may be tabulated from botanically determined plants represented by the various types of fossils. It is gratifying to note that so far as possible pollen grains are identified to extant taxa rather than lost to ecological implications in an arbitrary system of "artificial" nomenclature. From the various categories of fossils which have yielded botanical determinations it is evident that the early and mid-Tertiary forests of western Europe were rich in forms now extinct there, but currently surviving in part in the southeastern U. S. and in southeastern Asia. The brown coal flora hence represents a substantial supplement to a widely recognized distributional pattern of Holarctic warm-temperature forest types whose distribution retracted during the later Tertiary until many of their surviving representatives are limited to lower latitudes of warm temperate America and eastern Asia. It is the reviewer's opinion that the botanical work in these studies is excellent and forms a sound basis for the paleoecological and paleoclimatic interpretations set forth.

A somewhat unusual and slightly whimsical paleontological contribution is contained in the brief paper by Schmidt, Schuermann and M. Teichmueller dealing with the "Biss-Spuren" (bite-marks) of rodents and insects on the remarkably preserved lignitic fruits of the brown coal.

An impressive and very effective paleoecological summary of the collective paleobotanical evidence is presented by M. Teichmueller in dealing with reconstructions of the plant formations of the brown coal swamps. This paper is accompanied by three beautifully executed full color plates, showing the three major swamp and forest types deduced by the author to constitute the types of source vegetation leading to different facies of the brown coal. The three major swamp types proposed are "Everglades" type consisting of treeless grass-sedge marsh, the Taxodium-Nyssa forest swamp and the marginal Myrica-Cyrilla swamp with adjacent Sequoia forest. The critical reader may find these restorations a little too close to existing swamp types (with the exception of Sequoia) in the southeastern U. S. However, the botanical evidence presented seems quite convincing with possible exception of the quantitative importance of the "Everglades" type swamp or marsh in its ultimate contribution to the immense thickness of brown coal.

This impressive volume concludes with a chapter assaying present knowledge of the Lower Rhine basin and its remaining problems. The problems considered are chiefly stratigraphic and paleogeographic. In discussion of these questions, however, consideration is given to the paleoclimates of the period. It is of interest to note that a theoretical temperature curve deduced from paleontological evidence from early Eocene through the early Pliocene indicates a steadily declining temperature regime with slight upward deviation in the lower and middle Miocene. The rate of fall of temperature increases through the late Miocene and early Pliocene. This generalized concept of gradual climatic deterioration extending through the latter Cenozoic and culminating in the Pleistocene is quite consistent with comparable evidence from other paleobotanical studies in Europe and North America.

One of the more valuable attributes of this work is that it may serve as a guide or operational model for comparable intensive studies elsewhere. It likewise demonstrates how effectively a diverse range of disciplines extending from tectonics to palynology may be brought to bear in a synthesis of effort on a well defined geologic and paleontological investigation.

Elso S. Barghoorn

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[1] Teichmuller, R. and G. v. d. Brelie (editors). 1958. Die Niederrheinische Braun ohlenformation. (symposium) Fortschritte in der Geologie von Rheinland und Westfalen; herausgegeben von Wilhelm Ahrens. Geologisches Landesamt Nordrhein-Westfalen. Thomas-Druckerei, Kempen-Nordrhein. 763 pp., figs., halftones and 8 foldout maps. 58 contributors in 62 separate contributions.

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